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Rey Juan Carlos

TESIS DOCTORAL

Patrones y mecanismos determinantes de relaciones tritróficas (herbivoría de insectos y depredación por aves) a diferentes escalas espaciales

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“Fortunate are those who have learned to see, in the wild things of nature, something to be loved, something to be wondered at, something to be revered, for they will have found the key to a never-failing source of recreation and refreshment.”

Hugh B. Cott

Índice

1. Summary

Background

Plants and the herbivorous species linked to them represent 50% of the organisms on earth. The interactions that occur between them are key determinants of the structure of communities. All plant-based terrestrial communities are composed of three trophic levels that interact with each other: plants, herbivores and all the natural enemies of these herbivores (predators, parasites, and parasitoids). The interaction between these three levels constitutes the tritrophic interactions. Both herbivory and predation have been extensively studied in recent decades. Although there is extensive knowledge on the regulation of herbivory, the diversity of each host plant species' herbivores is significantly less explored. Only on tropical ecosystems there have been studies on the herbivorous diversity, their level of organization and specialization of trophic resources inside the host plant. In the Mediterranean region, although it is considered a hotspot for biodiversity, no studies of this kind have been done. The current species' distribution models, tools for climatic analysis, and the citizen science databases available can serve to complement knowledge of host specificity by herbivorous arthropods. On the other hand, and despite the extensive knowledge available on the regulation of insect predation, such as visual signals, there are hardly any studies that explore how this regulation varies between regions and over time, something that has been widely explored in the case of herbivory. Finally, although the information on herbivory variation at a global level is extensive and the effects of human impact on trophic relationships have been widely explored, there is no consensus about any of these regulatory factors for trophic interactions. Some studies point to an increase on trophic interactions in response to human disturbances, while others point to the opposite. There is also no consensus on how herbivory and predation can affect each other, since the human effect on one trophic group will consequently affect the rest. It is necessary to face this study with an approach that integrates all the variation collected in recent decades on a regional and global level, incorporating in the analysis new variables that can explain the regulation of trophic interactions considering all factors.

Objectives

This thesis aims to contribute in a general way to the knowledge about the diversity, organization and level of threat of herbivores in the Mediterranean region, the mechanisms of regulation of insect predation, such as visual signals, as well as their latitudinal variation, and the effects of human impact on trophic relationships. The specific objectives are: 1) To quantify the diversity of herbivorous arthropods of the holm oak (*Quercus ilex* L.), their feeding strategies and conservation status; 2) Investigate the relationships between the different herbivorous trophic groups of the holm oak and the taxonomic relationship between the species; 3) Evaluate the degree of host specificity for the phytophagous arthropod species that feed on holm oak, comparing their feeding strategies in different climatic niches; 4) Determine if the selection or avoidance of prey based on its color is consistent in space on a regional scale; 5) Quantify temporal patterns on the intensity of bird predation attacks; 6) Determine the variation on the selection or avoidance of prey based on its color on a global scale among different predators; 7) Study the impact pattern of urbanization on trophic interactions (herbivory of insects and predation by birds) at a global level; 8) Determine the latitudinal mechanism of regulation on trophic interactions (herbivory of insects and predation by birds) at a global level; and 9) Investigate the combined effects of human impact and latitudinal gradients on tritrophic interactions (insect herbivory and bird predation).

Methodology

Field work has been done in thirteen study areas in the center of the Iberian Peninsula with different degrees of management and proximity to population centers for three years to obtain information on the intensity and patterns of trophic interactions in Mediterranean ecosystems. To estimate predation, plasticine larvae of three colors were placed in most of the study areas, and of eight colors in two of them, on holm oak branches and, in two of the study areas, also on Montpellier maple and gum rockrose. The larvae were revisited monthly in the case of the three-color experiment, or weekly in the eight-color experiment, to estimate the intensity of predation and identify the predator. To quantify the herbivory, branches of three tree or shrub species that varied depending on the study area, but among which the holm oak was always included, were collected. Herbivory by invertebrates in leaves was estimated following widely used methodologies to enable its subsequent comparison. Statistical models for the estimation and comparison of climatic niches were used, as well as generalized and mixed linear models to explain the variation explained by our predictor variables. The different chapters of this thesis used different approaches that include the bibliographic review (Chapter 1), the analysis of the data collected in the field by the doctoral student during the completion of their doctoral thesis (Chapter 2), as well as the use of databases broader studies for the study of patterns and processes along latitudinal gradients (Chapters 3 and 4).

Results

The mechanisms and patterns that explain herbivory by insects and predation by birds have been studied at different spatial scales. Regarding the herbivory patterns of insects in the Mediterranean region, 605 species of invertebrate arthropods have been listed on the holm oak (*Quercus ilex*), of which 15 present some type of conservation threat. A phylogenetic relationship has been found in the organization of these herbivores on the different trophic resources of the plant, and it has been possible to identify host trophic specificity with holm oak in 20% of these species.

The mechanisms that apply to predation by birds regulated by the coloration of the prey have been explored, as well as the temporal patterns resulting from this regulation at the level of the center of the Iberian Peninsula. It has been possible to identify lower levels of predation in yellow and green larvae, regardless of the study area, in addition to patterns of variation in the intensity of this predation marked by an initial rapid decrease and a progressive increase throughout the weather. On a global scale, the mechanisms that affect the differential rates of predation depending on the color of the prey and latitudinal patterns have also been investigated, also identifying less predation in yellow larvae and variations in the rest of the colors in response to latitude.

Finally, and also at a global level, the mechanisms that affect both herbivory and predation have been studied, detecting latitudinal patterns and in response to human pressure. The results of our analysis indicate that herbivory and predation pressure increase with increasing population at high latitudes, while decreasing at low latitudes.

Conclusions

Holm oak is home to a large number of herbivorous arthropod species, supporting its role as a keystone species in Mediterranean forests. Species closely phylogenetically related to each other have similar foraging strategies, supporting the "taxonomic signal" hypothesis. Furthermore, we found a moderate degree of host specificity among these species (approximately 20%), but we did not identify a higher specificity for trophic groups.

Low attack rates on yellow larvae are a consequence of aposematism, while low attack rates on green larvae are due to crypsis. The rapid decline in attack rates by birds over time is probably the result of learning, and the increase in attacks in warmer months could be explained by the increase in chicks and migrant adults. Predation of herbivorous insects by birds increases from the Equator towards the poles, in a direction opposite to arthropod predation and opposite to the predictions of the atitudinal biotic interaction hypothesis. Also, they are affected differently by the color of the prey in different environments.

Herbivory and predation pressure increases with increasing population at high latitudes, while decreasing at low latitudes. This interaction effect between latitude and population density on trophic interactions can be explained by climatic changes produced by the heat island effect of cities, which allows greater activity of ectothermic arthropods in cold climates, while it can limit the survival of some species in hot climates.

2. Resumen

Antecedentes

Las plantas y las especies de herbívoros asociados a estas representan el 50% de los organismos de nuestro planeta. Las interacciones que se producen entre ellas son determinantes clave de la estructura de comunidades. Todas las comunidades terrestres basadas en plantas están compuestas por tres niveles tróficos que interactúan entre sí: las propias plantas, los herbívoros y todos los enemigos naturales de estos herbívoros (depredadores, parásitos y parasitoides). Las interacciones de estos tres niveles constituyen las relaciones tritróficas. Tanto la herbivoría como la depredación se han estudiado ampliamente en las últimas décadas. Pese a que se tiene un amplio conocimiento de cómo se regula la herbivoría, la diversidad de herbívoros de cada especie vegetal hospedadora está significativamente menos explorada. Solo en ecosistemas tropicales se ha llegado a estudiar la diversidad de insectos herbívoros, su organización y especialización por recursos tróficos dentro del árbol hospedador. En la región Mediterránea, pese a ser considerada un punto caliente de diversidad, no se ha realizado ningún estudio de este tipo. Los modelos actuales de distribución de especies, las herramientas de análisis climático y las bases de datos de colaboración ciudadana pueden servir para complementar los conocimientos sobre especificidad de hospedador por parte de artrópodos herbívoros. Por otro lado, y pese al amplio conocimiento disponible sobre regulación de la depredación de insectos, como las señales visuales, no hay apenas estudios que exploren cómo esta regulación varía entre regiones y en el tiempo, algo que si se ha explorado ampliamente en el caso de la herbivoría. Por último, aunque la información sobre variación de herbivoría a nivel global es amplia y los efectos del impacto humano sobre las relaciones tróficas han sido ampliamente explorados, no existe un consenso acerca de ninguno de estos factores de regulación de las interacciones tróficas. Algunos estudios apuntan hacia un incremento de las interacciones tróficas en respuesta a perturbaciones humanas, mientras otros apuntan a lo contrario. Tampoco existe consenso sobre cómo la herbivoría y la depredación, pueden afectarse entre sí, ya que el efecto humano sobre un grupo trófico necesariamente afectará al resto. Es necesario abordar este estudio desde un enfoque que integre toda la variación recogida en las últimas décadas a nivel regional y global, incorporando en los análisis nuevas

variables que puedan servir para explicar la regulación de las interacciones tróficas teniendo en cuenta todos los factores.

Objetivos

Esta tesis pretende contribuir de forma general al conocimiento sobre la diversidad, organización y nivel de amenaza de herbívoros en la región Mediterránea, los mecanismos de regulación de la depredación de insectos, como las señales visuales, así como su variación latitudinal, y los efectos del impacto humano sobre las relaciones tróficas. Los objetivos específicos son: 1) Cuantificar la diversidad de artrópodos herbívoros de la encina (*Quercus ilex* L.), sus estrategias de alimentación y estado de conservación; 2) Investigar las relaciones entre los diferentes grupos tróficos herbívoros de la encina y la relación taxonómica entre las especies; 3) Evaluar el grado de especificidad del hospedador para las especies de artrópodos fitófagos que se alimentan de encina comparando sus estrategias de alimentación en distintos nichos climáticos; 4) Determinar si la selección o la evitación de presas en función de su color es coherente en el espacio a escala regional; 5) Cuantificar patrones temporales en la intensidad de los ataques de depredación de aves; 6) Determinar la variación de la selección o la evitación de presas en función de su color a escala global entre distintos depredadores; 7) Estudiar el patrón de impacto de la urbanización sobre las interacciones tróficas (herbivoría de insectos y depredación por aves) a nivel global; 8) Determinar el mecanismo latitudinal de regulación de las interacciones tróficas (herbivoría de insectos y depredación por aves) a nivel global; y 9) Investigar los efectos combinados del impacto humano y gradientes latitudinales en las interacciones tritróficas (herbivoría de insectos y depredación de aves).

Metodología

Se ha trabajado en trece zonas de estudio del centro de la península ibérica con distintos grados de manejo y proximidad a núcleos de población durante tres años para obtener información sobre la intensidad y patrones de las interacciones tróficas en ecosistemas mediterráneos. Para estimar la depredación, se colocaron larvas de plastilina de tres colores, en la mayoría de zonas de estudio, y de ocho colores, en dos de ellas, en ramas de encina y, en dos de las zonas de estudio, también sobre arce de Montpellier y jara. Las larvas fueron revisitadas mensualmente, en el caso del experimento de tres colores, o semanalmente, en el de ocho colores, para estimar la intensidad de la depredación e identificar al depredador. Para cuantificar la herbivoría se recogieron ramas de tres especies de árboles o arbustos que variaron dependiendo de la zona de estudio, pero entre las que siempre se incluyó la encina. Se estimó la herbivoría por invertebrados en hojas siguiendo metodologías ampliamente utilizadas para posibilitar su posterior comparación. Se utilizaron modelos estadísticos de estimación y comparación de nichos climáticos, así como modelos lineales generalizados y mixtos para explicar la variación explicada por nuestras variables predictoras. Los diferentes capítulos de esta tesis utilizan diferentes abordajes que incluyen la revisión bibliográfica (Capítulo 1), el análisis de los datos tomados en campo por el doctorando durante la realización de su tesis doctoral (Capítulo 2), así como el uso de bases de datos más amplías para el estudio de patrones y procesos a lo largo de gradientes latitudinales (Capítulos 3 y 4).

Resultados

Se han estudiado los mecanismos y patrones que explican la herbivoría por insectos y depredación por aves a distintas escalas espaciales. Respecto a los patrones de herbivoría de insectos en la región mediterránea, se han listado 605 especies de artrópodos invertebrados sobre la encina (*Quercus ilex*), de las que 15 presentan algún tipo de amenaza de conservación. Se ha encontrado una relación filogenética en la organización de estos herbívoros en los distintos recursos tróficos de la planta y se ha podido identificar especificidad trófica de hospedador con la encina en el 20% de estas especies.

Se han explorado los mecanismos que aplican en la depredación por parte de aves regulados por la coloración de la presa, así como los patrones temporales resultado de esta regulación a nivel del centro de la Península Ibérica. Se han podido identificar menores niveles de depredación en larvas de color amarillo y de color verde, independientemente de la zona de estudio, además de patrones de variación de la intensidad de esta depredación marcados por una disminución rápida inicial y un aumento progresivo a lo largo del tiempo. A escala global, también se han investigado los mecanismos que afectan a las tasas diferenciales de depredación dependiendo del color de la presa y patrones latitudinales, identificando también menor depredación en larvas amarillas y variaciones en el resto de colores en respuesta a la latitud.

Por último, y también a nivel global, se han estudiado los mecanismos que afectan tanto a herbivoría como a depredación, detectando patrones latitudinales y en respuesta a la presión humana. Los resultados de nuestros análisis indican que la presión de herbivoría y depredación aumenta con el aumento de población en latitudes elevadas, mientras que disminuye en latitudes bajas.

Conclusiones

La encina alberga una gran cantidad de especies de artrópodos herbívoros, lo que respalda su papel como especie clave en los bosques mediterráneos. Las especies estrechamente relacionadas filogenéticamente entre sí tienen estrategias de alimentación similares, lo que apoya la hipótesis de la "señal taxonómica". Además, encontramos un grado moderado de especificidad del hospedador entre estas especies (aproximadamente el 20%), pero no identificamos una mayor especificidad por grupos tróficos.

Las bajas tasas de ataque en larvas amarillas son consecuencia del aposematismo, mientras que las bajas tasas de ataque larvas verdes se deben a la cripsis. La rápida disminución de las tasas de ataque por parte de aves a lo largo del tiempo es probablemente el resultado del aprendizaje, y el aumento de los ataques en los meses más cálidos podría explicarse por el aumento de polluelos y de adultos migrantes. La depredación de insectos herbívoros por aves aumenta desde el Ecuador hacia los polos, en una dirección opuesta a la depredación de artrópodos y opuesta a las predicciones de la hipótesis de interacción biótica latitudinal. Además, se ven afectados de manera diferente por el color de la presa en diferentes ambientes.

La presión de herbivoría y depredación aumenta con el aumento de población en latitudes elevadas, mientras que disminuye en latitudes bajas. Este efecto de interacción entre la latitud y la densidad de población sobre las interacciones tróficas puede explicarse por los cambios climáticos producidos por el efecto isla de calor de las ciudades, que permite una mayor actividad a los artrópodos ectotermos en climas fríos, mientras que puede limitar la supervivencia de algunas especies en climas cálidos.

3. Introducción general

Las plantas y las especies de herbívoros asociados a estas representan el 50% de los organismos de nuestro planeta y las interacciones que se producen entre ellas son determinantes clave de la estructura de comunidades a nivel mundial (Coley, 1998). Todas las comunidades terrestres basadas en plantas están compuestas por tres niveles tróficos que interactúan entre sí: las propias plantas, los herbívoros y todos los enemigos naturales de estos herbívoros (depredadores, parásitos y parasitoides) (Price *et al*., 1980). Las interacciones de estos tres niveles constituyen las relaciones tritróficas. En este tipo de relación se enmarcan los mecanismos que operan de abajo a arriba ("bottom-up") y los de arriba abajo ("top-down") en los ecosistemas. Los "bottom-up", en los que las plantas indirectamente controlan los sucesivos superiores niveles tróficos (Vidal y Murphy, 2018) se dan, por ejemplo, en la defensa química de las plantas, en respuesta a la cual se produce una coevolución rápida tanto de herbívoros, al consumir plantas, como de sus depredadores, al consumir a sus presas, hacia toxinas menos potentes (Feeny, 1976). Por otro lado, los "top-down", en los que los depredadores controlan el resto de niveles tróficos (Vidal y Murphy, 2018), se presentan, por ejemplo, en los ecosistemas en los que hay gran diversidad de especies depredadoras, que son los que poseen una mayor diversidad de los sucesivos niveles tróficos (herbívoros y plantas), ya que los depredadores impiden que sea una sola especie la que monopolice los recursos (Paine, 1966).

Tanto la herbivoría como la depredación se han estudiado ampliamente en las últimas décadas. Una búsqueda bibliográfica en el buscador "Pubmed", realizada el 12 de septiembre de 2021, usando las palabras clave "*herbivory*" y "*predation*" resultó en un total de 9.021 y 108.457 artículos publicados respectivamente (Figura 1). El conocimiento científico respecto a la depredación es mucho mayor y empieza a aumentar décadas antes que el de herbivoría. Además, este último parece haber alcanzado una meseta, al menos en lo relativo al número de publicaciones. Sin embargo, al realizar la búsqueda bibliográfica enfocada en la herbivoría de insectos ("*insect herbivory*") y depredación por aves ("*bird predation*") se obtuvieron un total de 4.712 y 4.471 publicaciones respectivamente, desapareciendo las diferencias en el nivel de estudio entre tipos de relaciones tróficas aunque se mantuvieron las tendencias al alza del estudio de la depredación por aves y la de estancamiento de herbivoría de insectos. La proporción de conocimiento relativo a la herbivoría de insectos respecto al total es bastante alta, llegando a suponer el 50% de las publicaciones sobre este tema. En el caso de la depredación, aquella llevada a cabo por aves supone menos del 5% del total de publicaciones, pudiendo considerarse esta marginal dentro del estudio de este tipo de interacción.

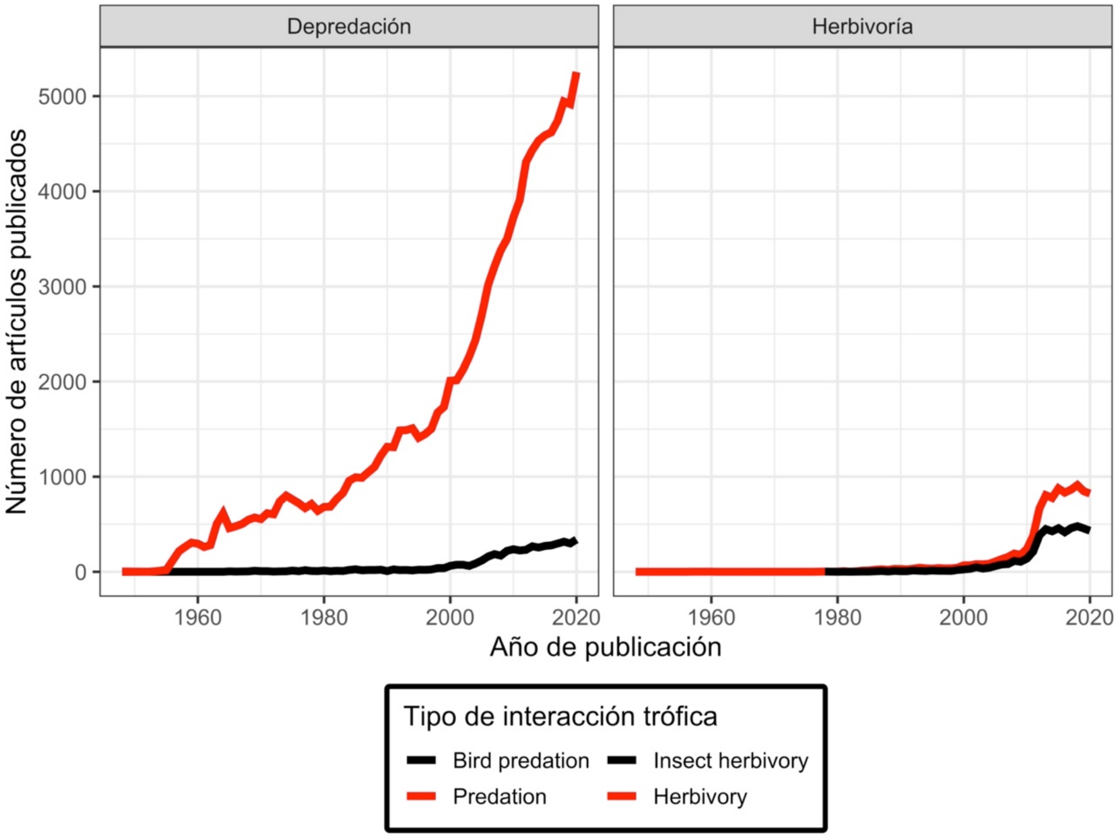

Figura 1: Número de artículos científicos por año de publicación resultado de una búsqueda en PubMed de los distintos tipos de interacciones tróficas utilizando diferentes palabras clave: "*Bird predation*", "*Predation*", "*Insect herbivory*" y "*Herbivory*". Fecha de la búsqueda: 12/09/2021.

3.1. Mecanismos de regulación

3.1.1. ¿Qué regula la herbivoría?

Son diversos los factores que regulan la herbivoría, entre ellos destacan la composición química de la planta, la época en la que se produce la herbivoría o la configuración espacial de la planta. Aunque la calidad nutricional de las hojas y los tallos puede influenciar la herbivoría, son las defensas químicas y estructurales los mayores determinantes de esta (Coley *et al.*, 1985). Las plantas pueden dividirse, según su tasa de crecimiento, entre aquellas de crecimiento rápido y las de crecimiento lento. Las de crecimiento lento son las que tienen una mayor inversión en defensas químicas, principalmente ligninas y polifenoles, como queda establecido en la hipótesis de disponibilidad de recursos (Coley *et al.*, 1985). Esta hipótesis explica que, en aquellos ecosistemas de recursos más limitados en los que las pérdidas ocasionadas por herbívoros son más costosas para la planta, los niveles de defensas anti herbivoría tendrán que ser necesariamente mayores. Por otro lado, a igualdad de biomasa comida por herbívoros, las plantas de crecimiento lento verán reducida en mayor proporción su producción neta que las de crecimiento rápido. Además de lo anterior, el coste energético de producir defensas ya sean químicas o estructurales, será menor en plantas de crecimiento lento. Por último, las especies con hojas de vida larga tienen una mayor concentración de químicos de defensa como taninos y ligninas (Coley, 1988).

La herbivoría también se puede ver afectada por la época en la que se produzca. En épocas secas la supervivencia de artrópodos herbívoros es menor (Coley, 1996), y hay especies vegetales que desarrollan sus hojas nuevas en esta época, y así experimentan la mitad de la herbivoría que aquellas que desarrollan las hojas en la época húmeda (Aide, 1993; Coley y Barone, 1996). Otras especies desarrollan en sincronía todas las hojas para, así, saturar a los herbívoros en recursos tróficos. Finalmente, las hay que tienen una rápida expansión foliar que minimiza el tiempo de exposición a herbívoros (Aide, 1993).

La herbivoría también puede variar dependiendo de la configuración espacial, por ejemplo, siendo mayor en el sotobosque que en las copas de los árboles. Esto se puede deber a nichos microclimáticos, al ser la copa mas cálida, seca y ventosa, y a diferencias en la composición de las hojas de sombra y las expuestas, siendo las segundas más pequeñas, duras y con mayor contenido fenólico (Lowman y Box, 1983; Coley y Barone 1996). Además, la depredación por aves es mayor en las partes abiertas del árbol que en las partes internas (Dial y Roughgarden, 1995), lo que puede influenciar la herbivoría ya que se ha demostrado una mayor tasa de defoliación por insectos al crear experimentalmente exclusiones para especies insectívoras (Dial y Roughgarden, 1995).

3.1.2. ¿Qué regula la depredación?

Es mucho mayor la información de que se dispone respecto a la regulación de la depredación que la de la herbivoría (Figura 1). Se han propuesto diversos mecanismos que determinan la selección de presas, entre los que destacan el comportamiento y tamaño de la presa, las señales químicas y la señalización visual. Respecto al comportamiento, las presas pueden desarrollar diversos mecanismos que pueden facilitar o dificultar la depredación, incluidas estrategias de movilidad (Sih y Christensen, 2001), de comportamiento de huida (Lang y Gsödl, 2001) o de realización de exhibiciones de amenaza que intimiden al depredador (Vallin *et al.*, 2006). Por otro lado, el tamaño de las presas también afecta a la depredación, ya que ayuda a la detectabilidad por parte de los depredadores, incrementando, por tanto, el riesgo de depredación. A su vez, un mayor tamaño aumenta la dificultad para capturarlas, lo que disminuye este riesgo (Pastork, 1981; Cogni *et al.*, 2002). Las señales químicas, como las feromonas, son de las señales más ampliamente extendidas, sobre todo, en relación con la señalización sexual. Las feromonas pueden ser utilizadas por las aves insectívoras a la hora de aumentar la efectividad de la depredación, ya que se ha demostrado que pueden ser percibidas por estas (Saavedra y Amo, 2018). Sin embargo, otras sustancias también potencialmente detectables por las aves, pueden ayudar a evitarla. Esta defensa química es una de las estrategias anti-depredación más utilizadas en orugas (Witz, 1990), aunque también suele ser la que energéticamente es más costosa, por lo que suele ir asociada a otras señales, como la señalización visual.

Tanto el tamaño como el comportamiento se ven influenciados por los mecanismos anti-predatorios relacionados con la señalización visual. Estos mecanismos se dividen en tres: i) la presencia de estructuras anti-predatorias, ii) el camuflaje, y iii) los colores aposemáticos. Una de las estructuras anti-depredadoras más comunes es la presencia de ocelos, que, a vista del depredador, pueden parecer ojos (Poulton, 1890). La presencia de estos patrones activa una respuesta innata de los depredadores, que se intensifica si existe un contraste entre el ocelo y el color de la presa (Hossie y Sherratt, 2012), y evita la depredación (Janzen *et al.*, 2010). Respecto al camuflaje, existen cinco principios generales que lo regulan: i) similitud del color con el fondo, ii) partes dorsales más oscuras que las ventrales, iii) presencia de coloración disruptiva, iv) eliminación de la sombra, y v) imitación de algunos objetos (Cott, 1940). En esta línea, Edmunds y Grayson (1991) apuntaron hacia una presión selectiva de las aves hacia dos variedades de la misma especie de polilla de diferentes colores, en función de la especie de árbol de la que se alimentasen, por diferencias en su detectabilidad. La presencia de colores aposemáticos, colores adaptativos de las presas que indican al depredador el riesgo potencial de consumirlas (Ruxton *et al.*, 2004), también influye en la presión de depredación (Sillén-

Tullberg, 1985; Mallet y Singer, 1987). Los colores aposemáticos activan una respuesta innata en los depredadores (Coppinger, 1970; Lindström *et al.*, 1999), aunque esta estrategia puede variar en su eficacia con el tiempo (Mappes *et al.*, 2014). El color amarillo (Iniesta *et al.*, 2016; Lawrence y Nooan, 2018), rojo, naranja o blanco (Exernová *et al.*, 2006; Svádová *et al.*, 2009) podrían detectarse como señales anti-depredatorias.

3.2. Componente espacial en las relaciones tróficas

El clima es el principal impulsor de la distribución de las especies, aunque otros factores, ya sean abióticos, como los suelos, o bióticos, como depredadores o competidores, también pueden afectarla (Gaston, 2003). La latitud es uno de los componentes geográficos que en mayor medida determina el clima. En las áreas tropicales, la mayor productividad y menor estacionalidad posibilitan una mayor diversidad, ya que las formas de vida con comportamientos más "marginales" pueden sobrevivir y establecerse. Mientras, en zonas con una menor disponibilidad de nutrientes o una estacionalidad más marcada, como son las zonas templadas, disminuye la probabilidad de supervivencia de estas especies marginales (MacArthur, 1969). El clima, por tanto, tiene un efecto claro sobre la composición y la diversidad de las comunidades biológicas, por lo que es frecuente encontrar patrones de variación a lo largo de gradientes latitudinales (Fischer, 1960; Rosenzweig, 1995; Gaston, 1996; Brown y Lomolino, 1998; Hillebrand, 2004), pero también puede tenerlo sobre las interacciones tróficas, que son más intensas en los trópicos que en las zonas templadas (Coley y Barone, 1996; Schemske *et al.*, 2009). Esto se explica por la estabilidad climática de las latitudes bajas, que habría permitido mayores tasas de adaptaciones fisiológicas y morfológicas, incrementándose así la diversidad y, con ella, el número de interacciones (Fischer, 1960).

3.2.1. ¿Cómo varía geográficamente la herbivoría?

La herbivoría difiere geográficamente por factores abióticos que determinan la composición y fenología de las plantas, lo que se puede ver reflejado en patrones latitudinales. El tipo de herbivoría difiere entre zonas geográficas. Mientras que en zonas tropicales el 70% de la herbivoría se produce en hojas nuevas y en crecimiento, con mayor riqueza nutricional (Coley y Barone, 1996; Coley y Aide, 1991), en zonas templadas el 75% se produce en hojas maduras (Reichle *et al.*, 1973). Las hojas de especies tropicales tienen mayores niveles y mas variados de compuestos defensivos contra la herbivoría que las de especies templadas, lo que parece ser debido a una mayor presión evolutiva por la gran abundancia y diversidad de invertebrados herbívoros en los trópicos (Coley y Barone, 1996). Las especies de hoja caduca, características de latitudes superiores, tienen menores niveles de defensa de las hojas (Coley y Aide, 1991), aunque desarrollan otras estrategias para minimizar la herbivoría, que suele ser, sin embargo, mayor que en bosques húmedos (Coley y Barone, 1996). En zonas templadas, la herbivoría de hojas nuevas es menor ya que las hojas brotan cuando aún las poblaciones de insectos son pequeñas, mientras que esto no se produce en zonas tropicales, en las que no hay una estacionalidad tan marcada y las poblaciones de herbívoros se mantienen estables durante todo el año (Coley y Barone, 1996).

En cuanto a la latitud, se han encontrado tasas de herbivoría superiores en latitudes bajas en la costa atlántica de Estados Unidos (Pennings y Silliman, 2005), lo que va en línea con la teoría generalmente aceptada (MacArthur, 1969). Sin embargo, recientemente, un estudio realizado en un gradiente de 17º de latitud que estudió la defoliación de hojas por insectos en cuatro especies de árboles, encontró un menor porcentaje de herbivoría en latitudes bajas (Adams y Zhang, 2009). Para explicar estos resultados no se tuvo en cuenta la mayor presión depredadora que los herbívoros de estas especies sufren por parte de sus enemigos naturales según disminuye la latitud (Björkman *et al.*, 2011). En esta línea, un meta-análisis sobre el porcentaje de herbivoría consumido por insectos herbívoros realizado con mas de 300 estudios encontró un patrón de herbivoría con forma de campana desde las latitudes más bajas a las mas altas, con un pico de herbivoría en las zonas templadas (Kovlov *et al.*, 2015), lo que apuntaría a que la hipótesis anteriormente propuesta no se cumpliría en zonas tropicales, pero si en zonas templadas y frías.

3.2.2. ¿Cómo varía geográficamente la depredación?

Al contrario que en la herbivoría, la variación geográfica de la depredación está poco explorada. La depredación varía geográficamente por los ecosistemas predominantes en cada zona y los efectos que estos tienen en la percepción de señales visuales de regulación de la depredación. Una estima realizada en 2018 apuntaba a que más del 70% de la biomasa consumida por aves insectívoras se producía en bosques, mientras que, en las praderas, tierras de cultivo y desiertos su consumo era mucho más reducido. De las 500 toneladas métricas consumidas por aves insectívoras en todo el mundo, los bosques tropicales suponían el 20%, mientras que los bosques templados y de tundra presentaban una cifra significativamente menor (Nyffeler *et al.*, 2018). Por otro lado, se sabe que existen diferencias geográficas en la percepción de las señales anti-depredadoras (Exernová *et al.*, 2015) mediadas, por ejemplo, por el tipo de ecosistema. En bosques cerrados de zonas tropicales, las mariposas de tonos oscuros experimentan significativamente una menor depredación por aves que las de colores claros, diferencias que no se dan en bosques abiertos (Cheng *et al.*, 2018).

Un estudio a escala global demostró una mayor depredación por artrópodos en latitudes bajas de ambos hemisferios, pero este patrón no se observó en depredación por aves o mamíferos (Roslin *et al.*, 2017). Este estudio se realizó con larvas de plastilina simulando larvas de mariposa, un método utilizado ampliamente para estimar tasas de depredación (Allen *et al.*, 1998; Howe *et al.*, 2009; Remmel y Tammaru, 2009; Iniesta *et al.*, 2016; Molleman *et al.*, 2016; Muiruri *et al.*, 2016; Saavedra y Amo, 2018; Valdés-Correcher *et al.*, 2021). Por el contrario, un meta-análisis realizado con información de 57 artículos no encontraba diferencias en la tasa de depredación entre zonas ecuatoriales y latitudes mayores (Lövei y Ferrante, 2016). No obstante, los autores del trabajo apuntaron a la falta de conocimiento en diversas zonas del planeta para explicar estos resultados.

3.3. Impacto humano sobre los ecosistemas

El impacto humano es, hoy en día, el principal agente de cambio en la naturaleza. Por ejemplo, se ha constatado una disminución de biomasa, abundancia y diversidad de insectos en las últimas décadas (Hallman *et al.*, 2017; Seibold *et al.,* 2019). Las causas principales de esta disminución son el cambio climático, el cambio de uso de suelo, el uso de pesticidas, la deforestación, la contaminación, la pérdida de hábitat, la homogeneización de la biodiversidad y la introducción de especies exóticas. Estos últimos cuatro impactos humanos son causados principalmente por la urbanización (McKinney, 2002). Las ciudades afectan al medio ambiente en diversos aspectos, entre los que destacan la contaminación del aire, la modificación de ecosistemas, el cambio de uso del suelo, la modificación de los ciclos biogeoquímicos, la contaminación del agua, la gestión de residuos sólidos y el clima (Bai *et al.*, 2017), y tienen un efecto directo sobre la riqueza de especies (Fattorini, 2011). Además, según la hipótesis de la perturbación creciente de Gray (Gray, 1989), la urbanización puede afectar negativamente la intensidad de las interacciones tróficas, ya que, en ambientes estresantes como los urbanos, se reduce la diversidad y aumentan las especies oportunistas, lo que provoca la reducción de la depredación y la herbivoría.

3.3.1. ¿Cómo afecta el impacto humano a la herbivoría?

La urbanización puede modificar los procesos ecológicos que afectan a la herbivoría, mediante cambios abióticos como la temperatura o la composición química, o bióticos como, la composición de especies. El efecto isla de calor (sobrecalentamiento de las ciudades en comparación con ambientes no urbanos por el calentamiento rápido de superficies predominantes como el asfalto o los edificios y que puede llegar a suponer un aumento de 10ºC [Kim, 1992]), la disponibilidad de agua, la contaminación y la fragmentación (De Carvalho Guimarães *et al.*, 2014), afectan tanto a herbívoros como a sus plantas hospedadoras (Miles *et al.*, 2019) y, por tanto, a la herbivoría. Otros factores asociados a las ciudades, como el aumento de la concentración de CO_2 en la atmósfera puede parecer beneficioso para la producción vegetal, pero los efectos a largo plazo de la dilución del contenido en nitrógeno de la atmósfera de un 10-30% producen una disminución de la calidad de las hojas que acaba produciendo un aumento de la herbivoría hasta en un 40% (Coley, 1998). Además, puede producir una disminución en el contenido de sustancias alcaloides de defensa (basadas en nitrógeno), y el aumento de sustancias basadas en carbono (taninos) (Coley, 1998). Aunque algunos estudios apuntan a un aumento de la herbivoría por insectos en ciudades en comparación con zonas rurales (Dreistadt *et al.*, 1990; Hanks y Deno, 1993; Cregg y Dix, 2001), los estudios más recientes apuntan a que esta presión disminuye (Moreira *et al.*, 2019), siendo este efecto mayor en ciudades más grandes (Kozlov *et al.*, 2017) y en respuesta a la densidad de población humana (Meineke *et al.*, 2019). Esta disminución de la herbivoría se ha explicado por el aumento, a su vez, de la depredación tanto por insectos como por aves insectívoras (Kozlov *et al.*, 2017).

3.3.2. ¿Cómo afecta el impacto humano a la depredación?

Hay diversas evidencias que apuntan a que la urbanización afecta negativamente a la intensidad de la depredación, principalmente por el cambio de composición de especies hacia aquellas con dieta omnívora, que aprovecharían las fuentes de comida de origen humano, lo que reduce en última instancia la presión de depredación (Eötvös *et al.*, 2018). Esta disminución de la tasa de depredación se ha podido constatar en un estudio que determinó la reducción de depredadores de áfidos en el sur de Inglaterra en respuesta a un gradiente de urbanización (Rocha y Fellowes, 2018). Esta disminución de la depredación se da tanto en la depredación de insectos (Ferrante *et al.*, 2014), como de aves (Major *et al.*, 1996; Gering y Blair, 1999; Jokimäki y Huhta, 2000; Thorington y

Bowman, 2003), siendo mayoritaria la segunda. Sin embargo, y contrariamente a lo anteriormente propuesto, otros estudios apuntan a un aumento de la depredación en ciudades en comparación con entornos naturales (Posa *et al.*, 2007), lo que explican por el aumento de la detectabilidad de presas en ambientes alterados.

3.4. Vacíos de conocimiento

Pese a que se tiene un amplio conocimiento de cómo se regula la herbivoría, la diversidad de herbívoros de cada especie vegetal hospedadora está significativamente menos explorada. Solo en ecosistemas tropicales se ha llegado a estudiar la diversidad de insectos herbívoros, su organización y especialización por recursos tróficos dentro del árbol hospedador. En la región Mediterránea, pese a ser considerada un punto caliente de diversidad, no se ha realizado ningún estudio pormenorizado sobre la diversidad, organización y nivel de amenaza de herbívoros. Los modelos actuales de distribución de especies, las herramientas de análisis climático y las bases de datos de colaboración ciudadana pueden servir para complementar los conocimientos sobre especificidad de hospedador por parte de artrópodos herbívoros. Por otro lado, existe abundante bibliografía al respecto de qué señales visuales son más efectivas a la hora de evitar la depredación por aves, sin embargo, se sabe que estas señales pueden variar geográficamente. Además, también se pueden producir diferencias de percepción de estas señales a lo largo del tiempo, causadas por cambios de detectabilidad por el aumento de follaje o explicadas por los cambios en composición de especies. Pese al amplio conocimiento disponible sobre regulación de la depredación de insectos, como las señales visuales, no hay apenas estudios que exploren cómo esta regulación varía entre regiones y en el tiempo, algo que si se ha explorado ampliamente en el caso de la herbivoría. Por último, aunque la información sobre variación de herbivoría a nivel global es amplia y los efectos del impacto humano sobre las relaciones tróficas han sido ampliamente explorados, no existe un consenso acerca de ninguno de estos factores de regulación de las interacciones tróficas. Algunos estudios apuntan hacia un incremento de las interacciones tróficas en respuesta a perturbaciones humanas, mientras otros apuntan a lo contrario. Tampoco existe consenso sobre cómo la herbivoría y la depredación, pueden afectarse entre sí, ya que el efecto humano sobre un grupo trófico necesariamente afectará al resto. Es necesario abordar este estudio desde un enfoque que integre toda la variación recogida en las últimas décadas a nivel regional y global, incorporando en los análisis nuevas variables que puedan servir para explicar la regulación de las interacciones tróficas teniendo en cuenta todos los factores.

3.5. Objetivos

En esta tesis se persiguen los siguientes objetivos.

1. Cuantificar la diversidad de artrópodos herbívoros de la encina (*Quercus ilex* L.), sus estrategias de alimentación y estado de conservación (Capítulo 1).

2. Investigar las relaciones entre los diferentes grupos tróficos herbívoros de la encina y la relación taxonómica entre las especies (Capítulo 1).

3. Evaluar el grado de especificidad del hospedador para las especies de artrópodos fitófagos que se alimentan de encina comparando sus estrategias de alimentación en distintos nichos climáticos (Capítulo 1).

4. Determinar si la selección o la evitación de presas en función de su color es coherente en el espacio a escala regional (Capítulo 2).

5. Cuantificar patrones temporales en la intensidad de los ataques de depredación de aves (Capítulo 2).

6. Determinar la variación de la selección o la evitación de presas en función de su color a escala global entre distintos depredadores (Capítulo 3).

7. Estudiar el patrón de impacto de la urbanización sobre las interacciones tróficas (herbivoría de insectos y depredación por aves) a nivel global (Capítulo 4).

8. Determinar el mecanismo latitudinal de regulación de las interacciones tróficas (herbivoría de insectos y depredación por aves) a nivel global (Capítulo 4).

9. Investigar los efectos combinados del impacto humano y gradientes latitudinales en las interacciones tritróficas (herbivoría de insectos y depredación de aves) (Capítulo 4).

3.6. Referencias

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4. Métodos generales

4.1. Lugares de estudio

Gran parte de los datos utilizados en esta tesis fueron tomados por el doctorando en doce localidades de bosque mediterráneo (Figura 2) ubicados dentro de un rango de latitud de 1,4º en el centro de la Península Ibérica, repartidas entre las provincias de Madrid, Toledo, Ciudad Real y Cáceres (Figura 3).

Monte de Viñuelas (Prístino)
Academia de Infantería (Prístino)
Finca la Alberquilla (Prístino)
Encinar de San Pedro (Periurbano)
Fuente del Moro (Periurbano)
Olivar de Santa Fe (Periurbano)
Ermita de Navahonda (Prístino)
Arroyo el Brezoso (Prístino)
Vía Pecuaria (Prístino)
Dehesa de Navalquejigo (Manejado)
La Alcornoquera (Manejado)
Finca la Cansina (Manejado)

Figura 2: Fotografías de cada una de las zonas de estudio en bosque mediterráneo. Adicionalmente se incluyó una nueva localidad (Manzanares el Real) que, junto con la Ermita de Navahonda, fueron utilizadas para la realización de un estudio piloto para ver las preferencias de color en la depredación de larvas por parte de aves insectívoras (Capítulo 2). Los muestreos en esta localidad sólo se realizaron durante 2018.

Se establecieron seis localidades en áreas con algún tipo de manejo (tres en bosques fuertemente manejados o plantaciones, y tres dentro o en el área circundante de ciudades) y seis en áreas naturales o seminaturales con bajo manejo humano. Las localidades urbanas o periurbanas se encontraban cerca o en ciudades con una población >100.000 habitantes y, al menos una localidad, estaba cerca de una gran ciudad con más de 1.000.000 de habitantes. Dentro de cada región, las localidades se seleccionaron en un diseño emparejado entre área prístina y manejada / periurbana y cada par se seleccionó, al menos, a 10 km de distancia entre sí. En estas localidades se realizaron los muestreos descritos en las secciones 4.2 y 4.3 durante tres años (2018, 2019 y 2020).

El clima de las zonas de estudio es mediterráneo continental, caracterizado por inviernos lluviosos y suaves, y veranos secos y calurosos, con una gran variabilidad interanual. El tipo de suelo varía entre luvisoles y umbrisoles en las zonas de estudio de la Comunidad de Madrid, y luvisoles, regosoles y leptosoles en el resto de las localidades.

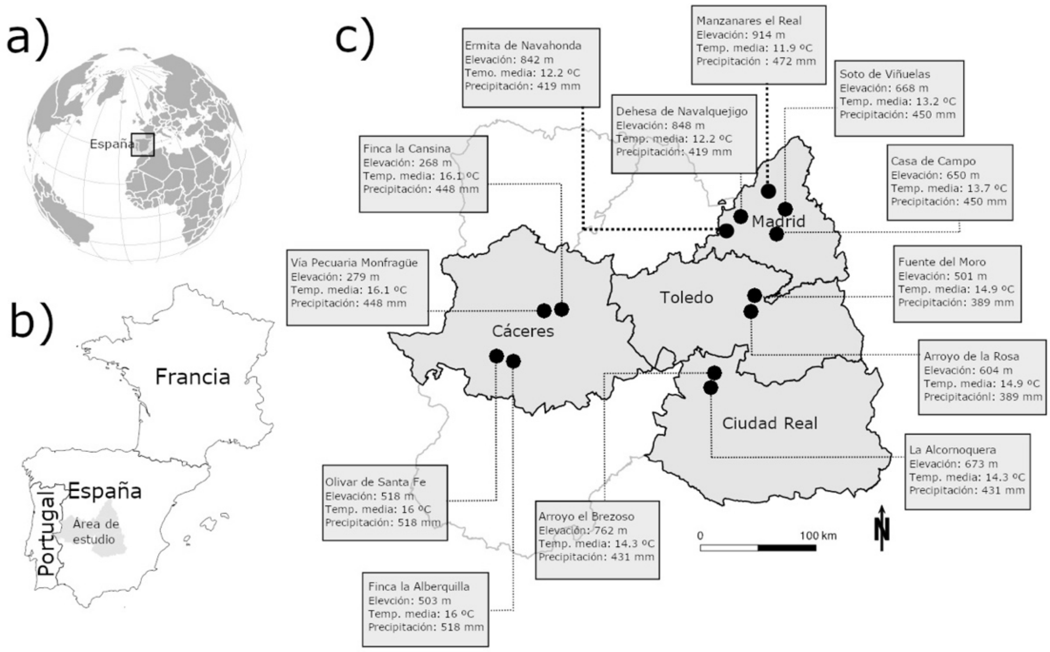

Figura 3: Mapa de las localidades de estudio donde se realizaron los muestreos de herbivoría por insectos y depredación por aves. En la localidad de Manzanares el Real se realizó sólo un estudio de depredación por aves como parte de un estudio piloto (Capítulo 2). Se muestra la situación de la zona de estudio a escala global (a), en la Península Ibérica (b), y a nivel de provincia (c). Para cada localidad se muestra la elevación, la temperatura media y la precipitación.

4.2. Herbivoría

La herbivoría de insectos se midió en cinco ejemplares de tres especies de árboles o arbustos por localidad y año de estudio. En todas las localidades estudiadas se incluyó a la encina (*Quercus ilex* L.) y las otras dos especies se seleccionaron según disponibilidad entre el alcornoque (*Quercus suber* L.), el fresno (*Fraxinus angustifolia* Vahl.), la cornicabra (*Pistacia terebinthus* L.), el espino negro (*Rhamnus lycioides* L.) o la jara (*Cistus ladanifer* L.). Los cinco individuos de cada especie vegetal dentro de cada localidad estaban separados entre sí al menos 15 metros. Para evitar sesgos sobre los valores de herbivoría, las ramas se seleccionaron estando a una distancia de 5–10 m de distancia, lo que no permite la evaluación visual previa del daño foliar. Las ramas seleccionadas para las mediciones de herbivoría eran accesibles desde el suelo (a una altura de 1-2 m) y tenían un mínimo de 50 hojas (Figura 4).

Figura 4: Metodología de recolección de ramas para la estimación de herbivoría.

Las ramas se colocaron dentro de una bolsa de malla transpirable y se transportaron al laboratorio, donde cada hoja se asignó a una de las siete clases de daño según el porcentaje del área foliar consumida por los invertebrados masticadores (0, 0.1-1, 1.1- 5, 5,1-25, 25,1-50, 50,1-75 y 75,1-100%; Figura 5) (Alliende, 1989; Kozlov *et al.*, 2015). El porcentaje total de herbivoría de cada rama se estimó multiplicando los valores medianos de cada clase de daño por el número de hojas en cada categoría dividido por el número total de hojas. Esta es una metodología estándar utilizada en otros estudios, lo cual permite la comparación con datos obtenidos por otros trabajos.

Figura 5: Metodología de clasificación de hojas según su nivel de herbivoría en el laboratorio.

4.3. Depredación

Se utilizaron larvas artificiales de plastilina para estimar la presión de depredación por depredadores sobre herbívoros. Las larvas artificiales se han probado ampliamente y han demostrado ser un método apropiado para investigar la depredación (Allen *et al.*, 1998; Howe *et al.*, 2009; Remmel y Tammaru, 2009; Iniesta *et al.*, 2016; Molleman *et al.*, 2016; Muiruri *et al.*, 2016; Saavedra y Amo, 2018; Valdés-Correcher *et al.*, 2021). Todas las larvas de plastilina se fabricaron con plastilina inodora (Chemical plant 'Luch', Yaroslavl, Russia) con un tamaño de 30 mm de largo y 4 mm de diámetro, y se utilizó un alambre de 0.5 mm enhebrado longitudinalmente para sujetar cada larva a una rama. Se utilizaron larvas de tres colores diferentes (marrón, verde y amarillo) en las 12 localidades de estudio, y larvas de ocho colores (negro, marrón, rojo, azul, verde, púrpura, blanco y amarillo) en las dos localidades utilizadas para el estudio piloto (Manzanares el Real y Ermita de Navahonda). Las larvas se colocaron en ramas delgadas (3-10 mm) a una altura de 1,5 a 2 metros (Figura 6) en cinco árboles o arbustos de encina (*Quercus ilex*) en las 12 localidades de estudio y en cinco ejemplares de tres especies (*Quercus ilex*, *Acer monspessulanum* L. y *Cistus ladanifer*) en las dos localidades utilizadas para el estudio piloto, a una distancia media aproximada de 30 cm entre sí (siempre al menos 20 cm de separación). Las larvas de plastilina expuestas a 30-50 cm de distancia para estudiar la depredación se consideran estadísticamente independientes entre sí (Tvardikova y Novotny, 2012; Bereczki *et al.*, 2014; Dattilo *et al.*, 2016).

Figura 6: Metodología de colocación de larvas de plastilina en ramas de encina.

Cada larva se expuso a los depredadores de 17 semanas a 6 meses. Las larvas fueron revisitadas mensualmente en el caso de las 12 localidades de estudio y semanalmente en el caso de las dos localidades en las que se realizó el estudio piloto (Figura 7). Cada vez que se visitaba una localidad, se verificaba la presencia de marcas de daños en cada larva y se asignaba a un tipo de depredador (ave, insecto o mamífero). Cuando se detectó algún daño, las larvas se repararon y moldearon en su forma inicial o se reemplazaron por nuevas si el daño era excesivo, siguiendo la metodología propuesta por Low *et al.* (2014).

Figura 7: Larvas de plastilina de diferentes colores (marrón, amarillo y verde) colocadas en ramas de encina por alambres con marcas de depredación causadas por aves.

4.4. Análisis estadísticos

Los análisis estadísticos realizados en esta tesis doctoral, excepto del capítulo 3, se llevaron a cabo enteramente en el ambiente de trabajo R (R Core Team, 2019) e incluyeron los paquetes: 'ade4' (Dray y Dufour, 2007), 'ape' (Paradis y Schliep, 2019), 'betareg' (Cribari-Neto y Zeileis, 2010), 'CoordinateCleaner' (Zizka *et al.*, 2019), 'DHARMa' (Hartig, 2019), 'ecospat' (Broennimann *et al.*, 2020), 'factoextra' (Kassambara y Mundt, 2017), 'glmmTMB' (Brooks *et al.*, 2017), 'lme4' (Bates *et al.*, 2015), 'MuMIn' (Barton, 2018), 'multcomp' (Hothorn *et al.*, 2008), 'pavo' (Maia *et al.*, 2019), 'raster' (Hijmans, 2020), 'rgbif' (Chamberlain *et al.*, 2020), 'sf' (Pebesma, 2018) y 'spdep ' (Bivand y Wong, 2018).

Para responder a diferentes preguntas de investigación a lo largo de la tesis, se ajustaron modelos lineales generalizados con distribución beta (Capítulo 1), y modelos lineales mixtos con distribuciones beta (Capítulo 4) y binomial (Capítulo 2). Para determinar los modelos con un mejor ajuste a los datos se realizaron comparaciones siguiendo el criterio de información de Akaike (Capítulos 2 y 4). Se estableció que un modelo era mejor que el resto si la diferencia entre el valor de AIC con el resto de modelos era superior a dos. Los análisis realizados en el capítulo 3 se realizaron en el software SAS/Stat. (SAS, 2009) y consistieron en modelos mixtos de análisis de la varianza. En todo caso se comprobaron los supuestos de homocedasticidad, normalidad y heterocedasticidad a través de los gráficos de los residuos de los modelos, se calcularon los valores de R^2 para modelos lineales generalizados y de R^2m (variabilidad explicada por los efectos fijos) y de R^2c (variabilidad explicada por los efectos fijos y aleatorios). También se hicieron comprobaciones post-hoc para determinar diferencias entre valores de las variables cualitativas predictoras (Capítulo 2). Por último, se realizaron análisis de autocorrelación espacial obteniendo el índice de Moran para los residuos de los modelos ajustados, con la información geográfica de cada zona de estudio (Capítulo 4). Se modeló el nicho climático utilizando análisis de componentes principales para resumir la información climática de las variables climáticas en solo dos valores con los que se calculó la similitud de nicho entre especies (Capítulo 1) y se llevaron a cabo análisis clúster para agrupar géneros de herbívoros en función de su recurso trófico y análisis de señal filogenética de recursos tróficos.

4.5. Referencias

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5. **Capítulo 1:** "What feeds on *Quercus ilex* L.? A biogeographical approach to studying trophic interactions in a Mediterranean keystone species."

Autores y filiaciones:
Juan Antonio Hernández-Agüero[1], Ildefonso Ruiz Tapiador[2] y Luis Cayuela[1].

1. Departamento de Biología y Geología, Física y Química Inorgánica, Universidad Rey Juan Carlos, Madrid, Spain
2. Departamento de Ingeniería Agroforestal, Universidad Politécnica de Madrid, Madrid, Spain

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What feeds on *Quercus ilex* L.? A biogeographical approach to studying trophic interactions in a Mediterranean keystone species

Juan Antonio Hernández-Agüero[1] | **Ildefonso Ruiz-Tapiador**[2] | **Luis Cayuela**[1]

[1]Departamento de Biología y Geología, Física y Química Inorgánica, Universidad Rey Juan Carlos, Madrid, Spain

[2]Departamento de Ingeniería Agroforestal, Universidad Politécnica de Madrid, Madrid, Spain

Correspondence
Juan Antonio Hernández-Agüero, Departamento de Biología y Geología, Física y Química Inorgánica, Universidad Rey Juan Carlos, c/ Tulipán s/n, E-28933 Móstoles, Madrid, Spain.
Email: hernandezaguer@gmail.com

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Abstract

Aim: Holm oak (*Quercus ilex* L.) is regarded as a keystone plant species. Trophic interactions may affect the distribution and abundance of phytophagous species, but the number of arthropod species that use holm oak as a food resource and their levels of host specificity are not yet known. Here, we aimed to quantify these species, their feeding strategies and conservation status, the taxonomic relatedness in each trophic guild and their degree of host specificity on holm oak.

Location: Our study covered the whole distribution area of *Q. ilex* in the central-western Mediterranean Basin.

Methods: We reviewed the existing literature and compiled information about all arthropod species that feed on *Q. ilex*, as well as their feeding strategies and conservation status. We also investigated the relationships between trophic guilds and the taxonomic relatedness of species, and assessed the degree of climatic niche overlap with holm oak.

Results: We found that 605 species feed on seven different parts of the holm oak plant (*i.e.* feeding strategies). More than 90% of these species lack a conservation status assessment, and eight are threatened by human activities, either as vulnerable, endangered or critically endangered. A significant phylogenetic relationship was found between taxonomic relatedness and groups of arthropods that feed on the same part of the plant (*i.e.* trophic guilds). Twenty per cent of the species had similar niches, thereby indicating the potentially high host dependence of these species.

Main conclusions: This study highlights the significance of a keystone tree species for arthropod conservation and the need for further research into the distribution and conservation status of arthropod species in Mediterranean holm oak woodlands.

KEYWORDS

arthropod biodiversity, climatic niche, feeding strategy, IUCN red list, phytophagous species, trophic guild

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1 | INTRODUCTION

The concept of keystone species was first proposed by Paine (1966) who suggested that certain species have impacts on many others, and often far more than those expected considering their biomass or abundance (Simberloff, 1998). Keystone species are distributed among various trophic guilds, including carnivores (Paine, 1969) [*e.g.* grey wolf (*Canis lupus)* or sea otter (*Enhydra lutris)* (Hale & Koprowski, 2018)], herbivores (Poelman & Kessler, 2016) [*e.g.* white-tailed deer (*Odocoileus virginianus*) (Waller & Alverson, 1997) and long-spined sea urchin (*Diadema antillarum*) (Lessios et al., 2001)], detritivores [e.g. Marion flightless moth (*Pringleophaga marioni*) (Haupt et al., 2014)] and primary producers (Terborgh, 1986) [*e.g. Azorella selago* (Nyakatya & McGeoch, 2008) and saguaro (*Carnegiea gigantea)* (Drezner & Balling, 2008)].

Among primary producers, species such as *Acacia peuce*, *Vachellia erioloba* and *Vachellia haematoxylon* can be considered keystone species in arid or semi-arid ecosystems (Nano et al., 2012; Shadwell & February, 2017; Tews et al., 2004). Large isolated trees belonging to these species can ameliorate harsh climatic conditions (Joffre et al., 1999) and increase soil nutrient levels (Joffre & Rambal, 1993; Munzbergova & Ward, 2002), plant species richness (Guevara et al., 1992) and structural complexity, as well as provide habitats for animals (Manning et al., 2006). Other trees that are considered keystone species include *Quercus douglasii*, *Sclerocarya birrea*, *Quercus griffithii*, *Schinziophyton rautanenii*, *Corymbia calophylla* and *Populus tremula* (Chidumayo, 2016; Helm & Witkowski, 2012; Kivinen et al., 2020; Paap et al., 2017; Rice et al., 1993; Singh et al., 2015). They provide resources (Messeder et al., 2020) and shelter to a large number of bird, mammal and insect species, some of which have a high degree of host specificity, that is specialization on host species used by phytophagous species (Ødegaard, 2004; Wardhaugh, Stork, & Edwards, 2012, 2013). Given the importance of these species for biological communities and considering the ongoing biodiversity crisis, conservation biology needs to devote more attention to identifying and conserving keystone species (Jordán, 2009).

The holm oak, *Quercus ilex* (Linneo, 1753), is considered a keystone tree species in the central-western Mediterranean Basin (Carnicer et al., 2014; Pérez-Ramos et al., 2013; Sirami et al., 2008). Holm oak not only represents a dominant species in Mediterranean woodlands and maquis vegetation, but can also form mixed stands throughout its distributional range (de Rigo & Caudullo, 2016). Holm oak forests have been reported to harbour high biodiversity in several taxa, including ectomycorrhizal fungi (Richard et al., 2005), lichens (Loppi & Frati, 2004) and plants (Díaz et al., 1997; Ihaddaden et al., 2013). Similar to other *Quercus* species in Mediterranean ecosystems, holm oak is suffering from the effects of a disease produced by the invasive oomycete *Phytophthora cinnamomi* (Brasier, 1996), which may have been increasing mortality since the 1980s (de Sampaio e Paiva Camilo-Alveset al., 2013). Holm oak-dominated dehesas ("human-made" ecosystems characterized by a savanna-like physiognomy used to maintain livestock and hunting activity, and to obtain other forest products) are also home to a large number of protected species (Díaz et al., 1997). In addition, holm oak may be an important trophic resource for various groups of organisms. In particular, Ruiz-Carbayo et al. (2017) identified 24 Lepidoptera species that feed on *Q. ilex* in Spain, and 86 saproxylic beetle species were reported to feed on holm oak trunks in France (Sirami et al., 2008). However, at present, it is not known how many arthropod species feed on *Q. ilex*, as well as the trophic guilds in which they are organized, or their host specificity.

It has been proposed that trophic guilds (*i.e.* a group of organisms with a similar feeding strategy) are phylogenetically conserved (Potapov et al., 2019). In arthropods, a relationship is expected between feeding strategies and taxonomy because feeding is known to be a significant driving force associated with evolutionary morphological changes (Maas et al., 2007). This relationship has been demonstrated in different families or orders of insects that preferentially feed on flowers, leaves, wood, fruits or sap, but mostly in tropical environments (Novotny et al., 2010; Wardhaugh, Stork, & Edwards, 2013, 2014). In addition, host specificity (*i.e.* the degree of host dependence) may affect the distribution of phytophagous insects, with highly specialized species exhibiting distributional ranges that are enclosed within the range of their host (Arnal et al., 2019; Du et al., 2020). In these cases, the climatic niche of the phytophagous species is expected to be constrained by that of the tree host. Host specificity has been shown to vary among arthropods with different feeding strategies ranging from the most specialized group comprising granivores to the least specialized group comprising root feeders (Novotny & Basset, 2005).

In this study, we aimed to review the importance of *Q. ilex* as a trophic resource for arthropods. In particular, our specific goals were as follows: (a) to quantify how many arthropod species feed on holm oak (*Q. ilex* L.), as well as assessing their feeding strategies and conservation status throughout its distributional range; (b) to investigate the relationships between trophic guilds and the taxonomic relatedness of species; and (c) to assess the degree of host specificity for phytophagous arthropod species that feed on holm oak by comparing their feeding strategies across climatic niches. We hypothesized that: (a) *Q. ilex* will provide food resources for a high number of arthropod species, thereby confirming its role as a keystone species; (b) closely related species will have similar feeding strategies compared with distantly related species in accordance with the "taxonomic signal" hypothesis (Potapov et al., 2019); and (c) host specificity will be widespread among arthropods that feed on holm oak, but higher for the most specialized feeding groups, such as acorn feeders. To the best of our knowledge, no previous studies have reviewed how many arthropod species feed on a keystone tree species in this much detail, and those that focused on investigations of trophic guilds were mostly conducted in tropical environments (Novotny et al., 2010; Wardhaugh et al., 2013, 2014). Trophic interactions are likely to fundamentally affect the distribution and abundance of organisms, so our results may provide a baseline and important insights regarding arthropod conservation in Mediterranean holm oak woodlands.

2 | MATERIALS AND METHODS

2.1 | Study species

Holm oak is a widespread tree or shrub, which has been historically managed as coppice forests or in pastures with large isolated trees (*i.e.* dehesas) where livestock feed on grass and acorns (Díaz et al., 1997). It can be found in the central-western part of the Mediterranean Basin from coastal zones to up to 1,800 m.a.s.l. in southern Spain or 2,900 m.a.s.l. in the High Atlas (Rigo & Caudullo, 2016). It is a shade-tolerant species and can grow in semi-arid to very humid climates.

Holm oak refers to two currently accepted species names comprising *Quercus ilex* L. and *Q. rotundifolia* Lam (Ferrer-Galego & Sáez, 2019). The latter is mostly distributed in the western Mediterranean, including the Iberian Peninsula and Morocco. There is a consensus that the morphological variation in these trees is very high and the taxonomic characters typically used to separate these two species (related to the shape, toughness and spinescence of the leaves) are extremely plastic, and thus of very limited value in taxonomy. Therefore, this complex was resolved at the subspecies level in the Iberian Flora (Castroviejo et al., 1990), where *Q. ilex* subsp. *ilex* L. is found in areas with a greater oceanic influence and *Q. ilex* subsp. *ballota* (Desf.) Samp. (*Q. rotundifolia*) is found in inland zones. Therefore, we use *Q. ilex* sensu lato to refer to either of these taxonomical interpretations at the species level (*Q. rotundifolia*) and/or the subspecies level (*Q. ilex* subsp. *ballota*).

2.2 | Study area

Our study covered the whole distribution area of *Q. ilex* in the central-western Mediterranean Basin (Figure 1), which is considered a major biodiversity hotspot (Myers et al., 2000). This area is characterized by a Mediterranean climate, with mild wet winters and warm-to-hot, dry summers (Lionello et al., 2006), and high human usage during the last 300 human generations (~7,500 years). This human usage is mainly characterized by forest management, agriculture and livestock production, or landscape modification, which led to the disappearance of 85% of the potential forest area (Blondel, 2006).

2.3 | Literature search

To quantify how many arthropod species feed on *Q. Ilex* and assess their feeding strategies and conservation status (goal 1), we conducted a literature search using Google Scholar, Dialnet, ResearchGate and Web of Science with pairwise combinations of the following two groups of keywords: "insect," "invertebrate" and "arthropod," and "*Quercus ilex*," "*Quercus rotundifolia*," "holm oak" and "evergreen oak," in English and the equivalent French, Italian or Spanish terms. These languages are spoken in at least eight out of the 17 countries where the holm oak is found, and they cover more than 90% of its distribution area. We reviewed all papers retrieved from the literature search and excluded studies that did not specifically report trophic interactions between arthropod species and *Q. ilex* regardless of the region where the study was conducted. We did not include pollinators in this study because *Q. ilex* is an anemophilous species. In addition to the literature search, we: (a) examined all references in the selected publications; (b) browsed all articles published in "Boletín de Sanidad Vegetal y Plagas," which is a Spanish journal published between 1975 and 2012 that focused on plant pest species, as well as all volumes of "Fauna Iberica" and "Faune de France" referring to terrestrial arthropods; and (c) reviewed all books available in the Rey Juan Carlos University (URJC), Madrid Autonomous University (UAM) and Madrid Polytechnic University (UPM) libraries covering aspects related to the feeding ecology of arthropod species in the Mediterranean region, including field guides. We annotated the parts of the plant consumed and geographical coordinates of the locations where arthropod species were recorded feeding on holm oak when available. We assumed that the identifications provided in the cited papers were correct without independent corroboration, although we checked for synonyms to avoid duplicating data. Finally, we conducted a search in the International Union for Nature Conservation (IUCN) Red List database (www.iucnredlist.

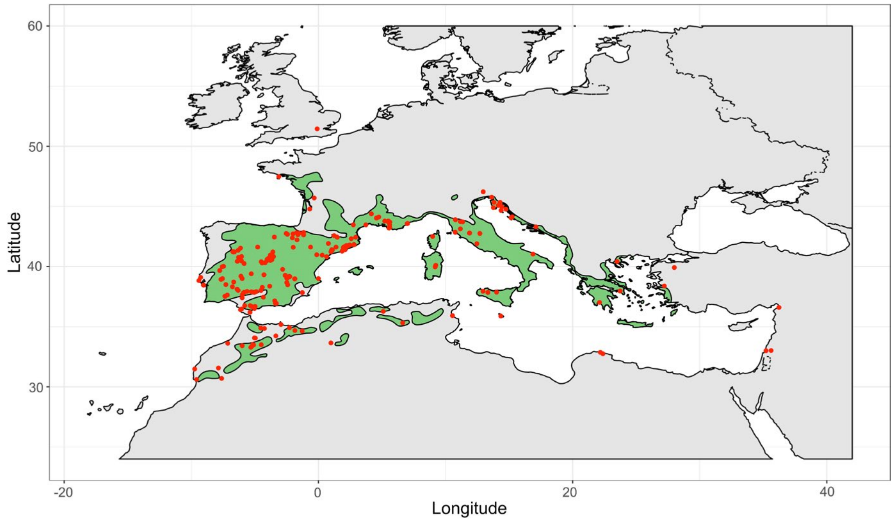

FIGURE 1 Study area and distribution of *Quercus ilex* (in green) based on Beck et al. (2020). Red dots represent the locations of studies that reported trophic interactions between holm oak and arthropod species based on our literature search. Dots outside the distributional range of *Quercus ilex* represent interactions in ornamental holm oaks

org) to retrieve information about the conservation status of each species found in our literature search.

2.4 | Investigating the relationships between trophic guilds and taxonomic relatedness

To investigate the relationships between trophic guilds and the taxonomic relatedness of species (goal 2), we conducted both phylogenetic and cluster analyses. We identified seven different feeding strategies: gall feeders (*i.e.* species that produce and feed via galls in leaves or stems), leaf feeders (including species that feed on both dead or living leaves and sprouts), wood feeders (including both xylophagous and saproxylic species that feed on trunks and stems), acorn feeders, sap feeders, root feeders and flower feeders.

We used the δ statistic (Borges et al., 2019) to test whether the feeding strategy was phylogenetically conserved. This metric measures the entropy contained in ancestral inferences in order to translate the principle of a phylogenetic signal into categorical data. Ancestral reconstructions using categorical data return the probability of each trait category occurring in each node (Borges et al., 2019). The δ statistic can be any positive real number, where a higher value indicates that the degree of a phylogenetic signal is higher between a given trait and the phylogeny. We used the phylogenetic tree published by Chesters (2017) and pruned it to include the phytophagous species associated with *Q. ilex* for which we had trophic information. To test for the statistical significance of δ, we randomized the feeding strategies of arthropods across the phylogenetic tree tips 200 times and compared the measured δ statistic (δ_{obs}) with the simulated statistic (δ_{sim}) to calculate a *p*-value.

We then conducted hierarchical cluster analysis to analyse the similarities of the feeding strategies among genera and to establish trophic guilds. The proportions of taxa with each feeding strategy were estimated at the genus level. We only used those genera and feeding strategies with more than three species for the analysis. If a species had more than one feeding strategy, we counted that species several times rather than using fractional assignment. Clustering was performed using the Manhattan dissimilarity measure and Ward's algorithm (Strauss & von Maltitz, 2017), and the optimal number of clusters was determined with the R package “factoextra” (Kassambara & Mundt, 2017) based on the k-means method with 999 bootstrap replicates (Monte Carlo resampling simulation).

2.5 | Environmental niche analysis

To assess the degree of host specificity for phytophagous arthropod species that feed on holm oak (goal 3), we estimated the climatic niche of both the holm oak and each arthropod species found in the literature search and calculated their climatic niche overlap. To achieve this, we downloaded the geographical coordinates of all records available for *Q. ilex* and *Q. rotundifolia* and their phytophagous arthropod species from the Global Biodiversity Information Facility (GBIF) using the R package “rgbif” (Chamberlain et al., 2020). The downloaded data were curated using the R package “CoordinateCleaner” (Zizka et al., 2019), which removed (0, 0) coordinates, sea coordinates and incorrect geolocations, such as records allocated to the centroids of countries or institutions where specimens were stored (*e.g.* herbaria at botanical gardens or universities), country capitals and identical coordinates (Figure 2). In addition, coordinates were aggregated to the resolution of the climatic variables (2.5 arc min) to avoid overrepresentation of locally clustered species records.

The climatic niche of each arthropod species and the holm oak was calculated for the same area, which encompassed most of Europe (excluding the northernmost part), northern Africa and western Asia, (24°N–60°N/18°W–42°E; Figure 1), and it included the entire distribution of holm oak. We downloaded 19 climatic raster layers from the WorldClim database (Hijmans et al., 2005) with a resolution of 2.5 min. We conducted principal component analysis (PCA) with all climatic variables across the entire study area (bounded area shown in Figure 1) using the R package “ade4” (Dray & Dufour, 2007) based on the method proposed by Broennimann et al. (2012). The first two PCA axes were used to quantify the observed climatic niches of species by creating a bidimensional representation of the environmental variables based on the 2.5-arc-min grid cells with records of species occurrences (Figure 2). To accurately estimate the climatic niches of species, we only used those species present in at least 30 cells (Franklin, 2010; Supplementary Material 1), with a total of 294 species. We evaluated the climatic niche overlap between holm oak and its phytophagous species using the R package “ecospat” (Figure 2; Broennimann et al., 2020). We ran similarity analyses to test the overlap of two niches using the D metric proposed by Schoener (1968), which ranges between 0 (no overlap) and 1 (complete overlap). Based on this metric, a similarity test was conducted with function “ecospat.niche.similarity.test” in R (Broennimann et al., 2020) to determine which of the arthropod species distributions was explained by the holm oak distribution (a host dependence relationship) (Warren et al., 2008). This analysis was conducted based on the assumption that climate is the main driver of species distribution, although it is important to consider that other factors can also affect species distribution, including abiotic factors such as soils, or biotic factors such as predators or competitors (Gaston, 2003). This similarity test comprised a background test to assess whether two niches were more or less similar than expected by chance. A permutation approach (using 100 permutations) was employed to assess the significance of tests, where a *p*-value $> .05$ indicated that niches were no more similar than expected by chance (i.e. different). We considered that the host specificity of an arthropod species was holm oak when the similarity test between the host and phytophagous species obtained a value that differed significantly from that expected by chance (*p*-value $< .05$) (Figure 2). This approach has been used widely in previous studies of patterns of future species stability (Molina-Henao & Hopkins, 2019), predictions of suitability for

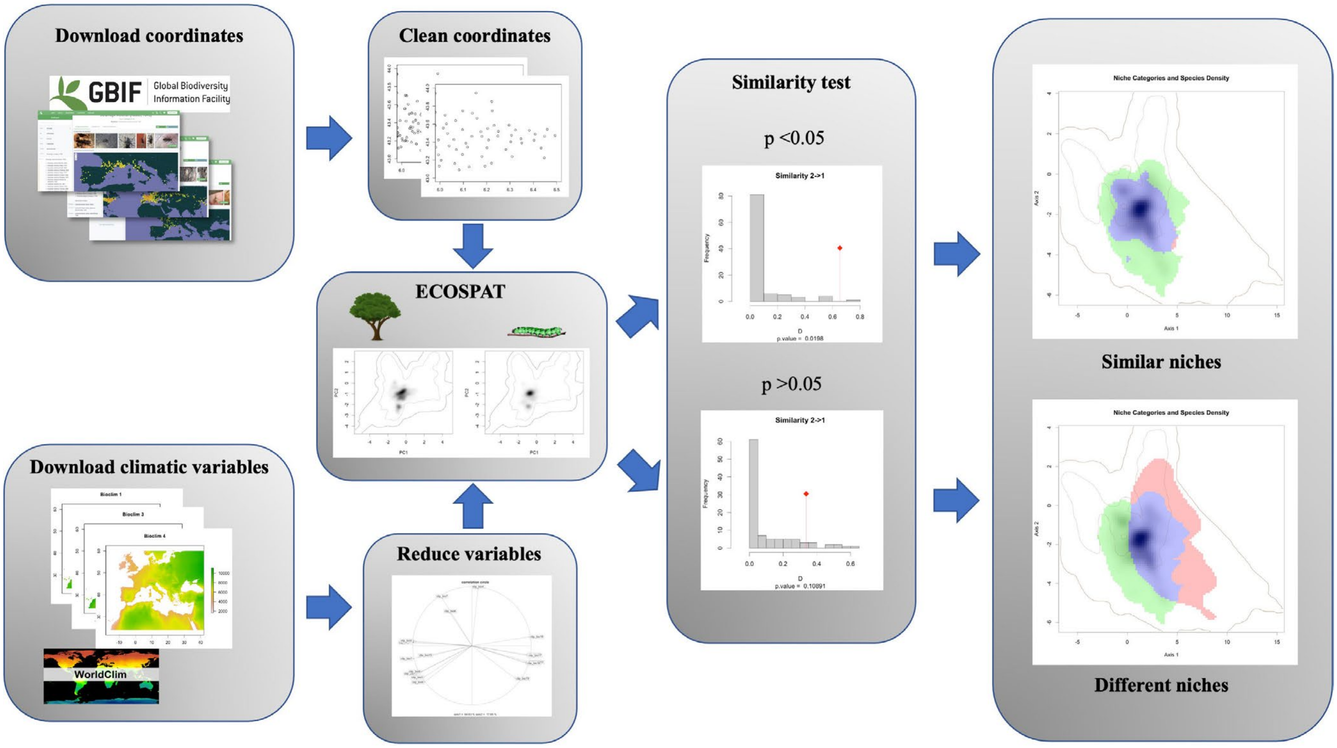

FIGURE 2 Workflow diagram illustrating the niche overlap analysis conducted in this study, data preparation and the possible outcomes in terms of similarity

invasive species (Beukema et al., 2018; Zemanova et al., 2018), spatial differentiation of subspecies (Ashrafzadeh et al., 2018), comparisons of climatic niches for species under present and future scenarios (Hamid et al., 2019), and assessing phytophagous species–host niche overlap (Arnal et al., 2019).

Finally, we fitted a generalized linear model with a beta error distribution to test for differences in Schoener's D metric among feeding strategies in order to assess differences in host specificity between feeding guilds. This analysis was conducted with the R package "betareg" (Cribari-Neto & Zeileis, 2010).

3 | RESULTS

3.1 | Literature search

We identified 605 species from 342 genera, 90 families and eight arthropod orders (Table 1; Hernández-Agüero et al., 2021) based on 198 sources found during the two years of consult (Figure S2a), including research papers (69%, *n* = 136) and books (31%, *n* = 62) (Supplementary Material 2: Figure S2c), with 271 (44.8%) species cited in research papers, 269 (44.4%) in books, and 75 (12.3%) in both sources. (A list of the data sources is found in Appendix 1.) We found bibliographic information from 17 different countries, where the highest number of sources came from Spain, followed by France and Italy (Figure S2b), which corresponds to the countries with the largest holm oak distributions (Figure 1).

TABLE 1 List of arthropod orders that feed on holm oak and families with the highest number of species. Numbers of species and their percentage relative to the total (605) are also presented for both orders (left) and families (right)

Order	Most common families	Number of species	% of species
Coleoptera		250	41.32
	Cerambycidae	72	11.86
	Curculionidae	50	8.24
	Chrysomelidae	42	7.24
	Buprestidae	35	5.77
Lepidoptera		157	25.95
	Geometridae	27	4.45
	Erebidae	20	3.29
	Noctuidae	16	2.64
Hemiptera		95	15.70
	Miridae	32	5.27
	Aphididae	22	3.62
Hymenoptera		75	12.39
	Cynipidae	35	5.77
Trombidiformes		12	1.98
Diptera		12	1.98
Psocoptera		2	0.33
Blattodea		2	0.33
TOTAL		605	

Among the 605 species found to feed on *Q. ilex*, 71 (11.73%) were included in the IUCN Red List with assessments conducted at the global (*n* = 11), European (*n* = 66) or Mediterranean geographical scope (*n* = 33) (Hernández-Agüero et al., 2021). At the global geographical scope, three species were identified as data deficient (DD), four as least concern (LC), two as near threatened (NT) and two as vulnerable (VU) (Table 2). At the European geographical scope, four species were identified as DD, 49 as LC, seven as NT, three as VU, two as endangered (EN) and one as critically endangered (CR). Finally, at the Mediterranean geographical scope, two species were identified as DD, 26 as LC, three as NT, one as EN and one as CR (Table 2).

3.2 | Feeding strategies

Among the 605 species included in this study, we obtained information about the feeding strategies of 527 species, where 42% fed on leaves (*n* = 222), 31% on wood (*n* = 164) and 13% on galls (*n* = 70), and 9% were sap feeders (*n* = 45). The remaining 5% of the species fed on flowers (*n* = 16), acorns (*n* = 10) and roots (*n* = 2). We found that 98% of the species fed only on one part of the *Q. ilex* plant, 1.3% on two parts and 0.5% on three or more parts. The pruned phylogenetic tree contained 205 out of the 527 species for which we obtained information about their feeding strategies (Figure 3). A strong phylogenetic signal was associated with feeding strategies ($\delta_{obs} = 1.582$, δ_{sim} 95% confidence interval = 0.881–1.179, *p*-value = 0.005).

Based on the feeding strategies of the different genera, we identified six major clusters (trophic guilds) with Ward's clustering algorithm. One of the two main partitions split into two clusters dominated by leaf feeders (Figure 4, purple and blue) in genera from Coleoptera (*Cryptocephalus*, *Polydrusus*, *Rhynchites*, *Coeliodes*, *Smaragdina*, *Pachybrachis*, *Lachnaia* and *Labidostomis*), Lepidoptera (*Catocala*, *Phyllonorycter*, *Eupithecia*, *Stigmella*, *Ectoedemia* and *Dryobotodes*) and Hymenoptera (*Periclista*). The second partition split into four clusters encompassing wood feeders in genera (Figure 4, turquoise) from Coleoptera (*Anthaxia*, *Agrilus*, *Trichoferus*, *Cerambyx*, *Purpuricenus*, *Rhagium* and *Clytus*); sap feeders (Figure 4, green) in genera from Hemiptera (*Myzocallis* and *Kermes*); acorn feeders (Figure 4, brown) in genera from Trombidiformes (*Aceria*), Lepidoptera (*Cydia*) and Coleoptera (*Curculio*); and gall feeders (Figure 4, pink) in genera from Hymenoptera (*Plagiotrochus*, *Andricus*, *Mesopolobus* and *Synergus*) and Diptera (*Contarinia*). Flower feeders did not constitute a cluster but they were present in others.

3.3 | Environmental niche analysis

Records were available in the GBIF for 491 (80%) of the 605 arthropod species that feed on *Q. ilex*, but only 294 species had a sufficiently high number of records ($n > 30$, ~48%) to reliably estimate their environmental niche, with a range between 31 and 13,149 records, and a mean of 1,136 coordinates per species. The first and second principal components obtained by PCA explained 64.63% and 17.65% of the climatic variation, respectively. Only 53 (18.02%) of the species studied had similar climatic niches (*p*-value < .05) to *Q. ilex* (see Figure 5 for an example). All of the climatic niche analysis results are available in Supplementary Material 3.

Finally, we found no statistically significant differences in the degree of overlapping with the climate niche of holm oak among arthropod feeding strategies (*p*-value = 0.275).

TABLE 2 List of species evaluated under the IUCN Red List criteria at different geographical scopes (global, European and Mediterranean), excluding the data deficient (DD) and least concern (LC) categories

Species	Global	European	Mediterranean
Alocerus moesiacus (Frivaldszky, 1837)		NT	
Alocerus siculus (Sama, 1979)		CR	CR
Bothrideres interstitialis (Heyden, 1,870)			EN
Brachygonus megerlei (Lacordaire, 1835)		NT	
Calchaenesthes sexmaculata (Reiche, 1861)	NT	EN	NT
Cerambyx cerdo (Linneo, 1758)	VU	NT	LC
Cerambyx dux (Faldermann, 1837)		NT	LC
Cerambyx miles (Bonelli, 1823)		NT	LC
Cerambyx welensii (Kuster, 1846)		NT	NT
Chlorophorus favieri (Fairmaire, 1873)	NT		NT
Lichenophanes varius (Illiger, 1801)		NT	
Necydalis ulmi (Chevrolat, 1838)		VU	
Pachyta lamed (Linnaeus, 1758)		VU	
Pedostrangalia revestita (Linnaeus, 1767)	VU	VU	
Stictoleptura oblongomaculata (Buquet, 1,840)		EN	

Abbreviations: CR, critically endangered; EN, endangered; NT, near threatened; VU, vulnerable.

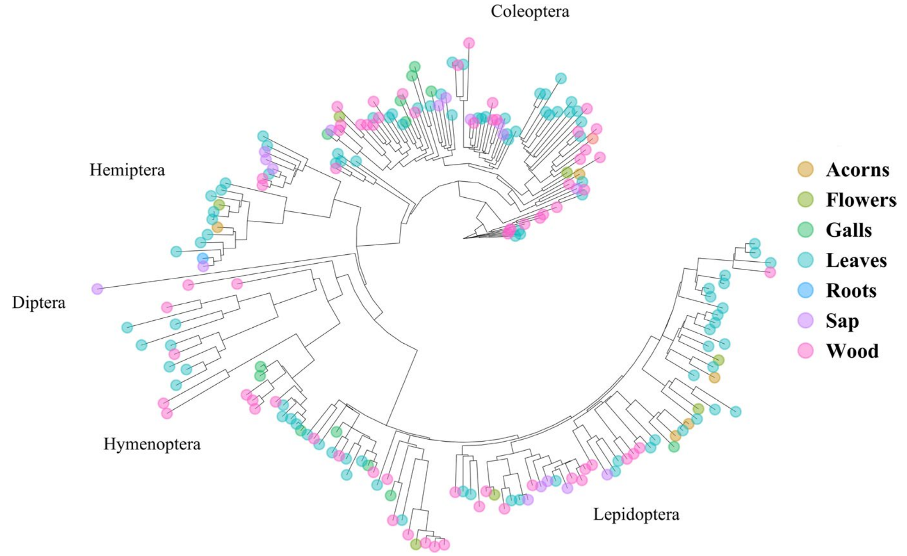

FIGURE 3 Phylogenetic tree pruned from Chesters (2017), where 205 of the 605 species found in the literature search were included in the phylogenetic tree with trophic information. Trombidiformes, Blattodea and Psocoptera species are not represented in the tree. Different colours are used to represent the feeding strategy of each species at the tree tips

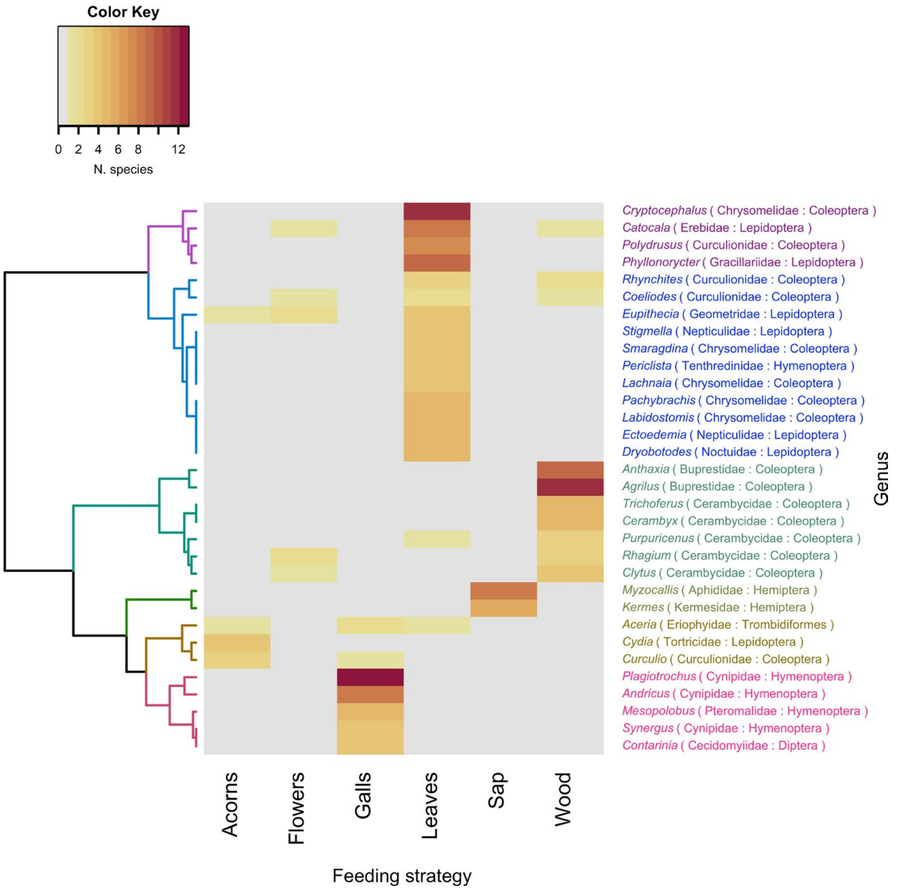

FIGURE 4 Hierarchical clustering showing the similarity of feeding strategies among arthropod genera that feed on *Quercus ilex*. Rows represent arthropod genera (family and order in brackets), and columns represent feeding strategies. The colour key is proportional to the number of species in each genus. The dendrogram on the left-hand side shows six major clusters of trophic guilds represented by different colours from top to bottom: purple, blue, turquoise, green, brown and pink

4 | DISCUSSION

Based on our literature analysis, we found more than 600 species that feed on holm oak (*Q. ilex*). More than 90% of the species lack a conservation status assessment, where only 71 of the species were found in the IUCN Red List, with 56 in the DD category. Among the other 15 species, eight species are threatened by extinction at either global, European or Mediterranean geographical scopes. Most of the species feed on leaves, wood, sap or galls, and about 20% of the arthropod species were found to have niche similarity to holm oak, but we detected no differences in niche overlap between feeding strategies.

4.1 | Arthropod species that feed on holm oak

Tropical tree species can sustain a high number of arthropod species. For example, the number of phytophagous Coleoptera species

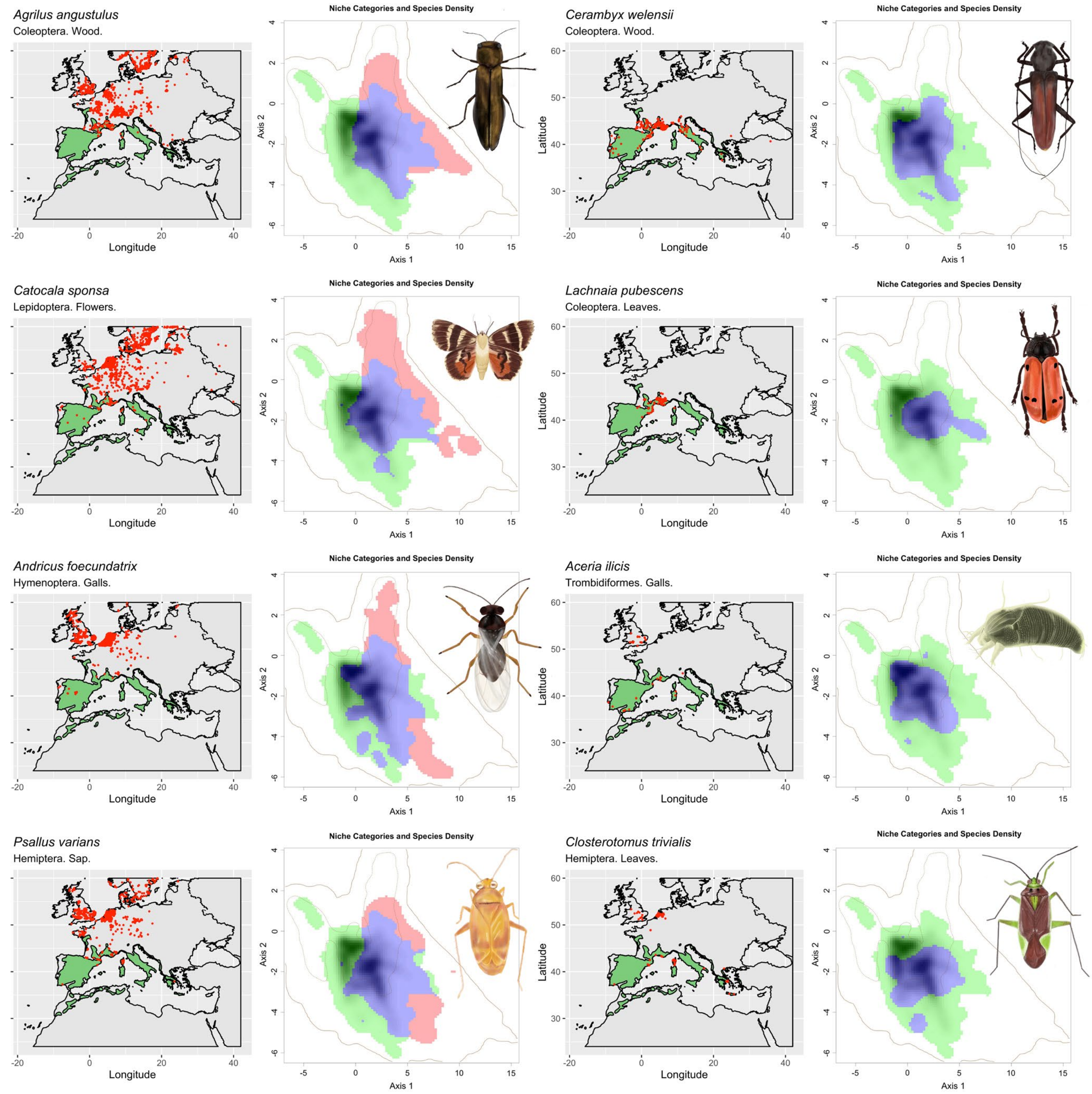

FIGURE 5 Examples of the distributions of eight species representing different orders and feeding strategies (red dots) used for niche overlap analysis. Green shows the distribution of *Quercus ilex*. The two first columns represent species with a different climatic niche to holm oak, and the last two columns represent species with a similar climatic niche to holm oak. Comparisons of the climatic niches are shown between holm oak (in green) and phytophagous species (in red) for every species. The niche overlap between species is represented in blue. Drawings of species by I. M. Alonso-Crespo

found on *Brosimum utile* in tropical forests across the Neotropics was estimated as ca. 900 (Ødegaard, 2004), which contrasts with the 250 Coleoptera species found in our study. However, the amounts of species are much lower in temperate ecosystems. For example, based on a literature review, it was proposed that two oak species in the UK can support ca. 300 insect herbivore species (Southwood, 1961). However, in the present study, we found that over twice that amount of species feed at least partially on *Q. ilex*, thereby indicating a high level of biodiversity, at least compared with other oak species in temperate ecosystems. This number should not be treated as the actual amount because many species have yet to be formally described and catalogued (Whittaker et al., 2005), while others may have not been observed feeding on holm oak and/or reported in the scientific literature, and finally, our knowledge of the global, regional and even local distributions of many taxa, particularly arthropods, is far from being complete (Lomolino, 2004). In addition, it should be noted that each arthropod species that feeds on holm oak can easily attract an average of 5–15 parasitoids and predators (Price, 2002), and thus, the number of arthropod species indirectly supported by holm oak woodlands might potentially range between 3,650 and 9,750 based on current figures for known taxa. This estimate only considers direct and indirect trophic interactions, and it could be higher if we consider species that use holm oak for shelter. *Q. ilex* is also known to be suitable for the establishment of other non-arthropod species, including lichens (Loppi & Frati, 2004), fungi (Richard et al., 2005) and vertebrates (Díaz et al., 1997). Overall, our results support the role of holm oak as a keystone tree species in Mediterranean ecosystems, as shown in previous studies (Carnicer et al., 2014; Pérez-Ramos et al., 2013; Sirami et al., 2008).

4.2 | Is there a relationship between the degree of feeding strategies and taxonomic relatedness of species?

Our results indicated a relationship between the feeding strategies and taxonomic relatedness of species, and this is in agreement with the "taxonomic signal" hypothesis, which suggests that closely related species have more similar species' traits compared with distantly related species (Potapov et al., 2019). However, our results indicated some variability in the phylogenetic composition of some trophic guilds, especially between acorn feeders, possibly as a response to strong trophic competition within taxonomically related species only allowing the coexistence of some phytophagous species, that is only 10 species in our study. This can be explained by the "limiting similarity" hypothesis (Potapov et al., 2019). Thus, many taxonomic groups seem to have developed specialized feeding strategies, such as Buprestidae, Cerambycidae and Cynipidae, whereas others have not, including Curculionidae.

The two trophic guilds of leaf feeders mostly comprised genera from Coleoptera and Lepidoptera, as well as one genus from Hymenoptera (Figure 4). These results are similar to those obtained by Novotny et al. (2010) in tropical forests, although they also found a substantial number of Orthoptera and Phasmatodea species with the leaf-feeding strategy, whereas these orders were not found to feed on holm oak. The trophic guild dominated by wood feeders in our study mostly comprised genera from Coleoptera in a similar manner to previous studies conducted in tropical forests (Novotny et al., 2010; Wardhaugh et al., 2013). The use of wood as a food resource appeared to be dominated by this order of insects. Indeed, dehesas (the most representative holm oak ecosystem) are considered a key ecosystem for saproxylic feeders (Ramírez-Hernández et al., 2014), and this might explain why we detected a disproportionate number of species that feed on this resource (wood) compared with other holm oak plant parts. In addition, the wood obtained from holm oak is economically important and much research has been conducted to minimize the economic losses caused by insect pests during its production. The trophic guild dominated by sap feeders entirely comprised Hemiptera species. A previous study also found that Hemiptera species are the most important sap feeders in tropical forests (Novotny et al., 2010), probably due to the highly specialized structures that they have evolved to obtain this resource (Goodchild, 1966). In contrast to our findings for other trophic guilds, the guild dominated by acorn feeders did not exhibit a taxonomic clustering pattern. The number of species that feed on this resource was relatively low and most belonged to three genera. The gall feeder trophic guild is extensive on holm oak (see references by Nieves-Aldrey in Hernández-Agüero et al., 2021), and we found that it mainly comprised genera from Cynipidae, a highly specialized family in the production of galls. Flower feeders did not constitute a trophic guild. Root feeders were not considered in our analysis due to the low number of species found, and the lack of literature regarding this trophic guild might have led to underestimation of the proportion of species that use this resource. However, it has been shown that this trophic guild has the lowest level of host specificity (Novotny & Basset, 2005).

4.3 | Does environmental niche overlap occur between holm oak and phytophagous arthropods?

Among the 294 species considered for niche analysis, we found that 53 (18.02%) exhibited niche similarity to holm oak. Niche similarity indicates climatically driven species co-occurrence patterns that might be caused by different underlying ecological processes. For example, some of the arthropod species that exhibited niche similarity to holm oak might depend entirely on this resource because they have developed specificity for this host as a resource, for example *Satyrium esculi* or *Plagiotochus quercusilicis*. In contrast to our expectations, no differences in niche overlap were detected between feeding strategies, although this pattern might have been obscured by: (a) the lack of relevant data for specific trophic guilds such as root feeders, which typically exhibit less host specificity (Novotny & Basset, 2005); and (b) the possible influence of microhabitats on arthropods climatic niches, which could not be accurately depicted with the spatial resolution of the WorldClim climatic layers used in this study.

4.4 | Prospects for arthropod conservation

Quercus ilex is currently threatened by the invasive fungal species *Phytophthora cinnamomi* (Brasier, 1996; de Sampaio e Paiva Camilo-Alves et al., 2013), drought-induced tree mortality (Gea-Izquierdo et al., 2011), lack of regeneration (Plieninger et al., 2010; Pulido & Díaz, 2005) and land use changes (de Rigo & Caudullo, 2016). These threats have reduced the distribution of holm oak to ca. 22% of its potential distribution, at least in the Iberian Peninsula (Felicísimo et al., 2012). Thus, our results highlight the vulnerability of arthropod species that feed on this keystone species, particularly for species with small geographical ranges or population sizes. However, details are lacking regarding basic aspects of the ecology of most arthropod species, such as where a species is found, which contrasts sharply with other groups such as mammals, birds, reptiles and plants (Cardoso et al., 2011). Thus, insufficient data were available to reliably describe the distributional ranges of more than 50% of the arthropod species. The lack of information was even more obvious when we considered the conservation status of the arthropod species because conservation status assessments were not available for over 90% of the species. Among the 71 species with full conservation assessments, 15 were threatened by extinction at global, European or Mediterranean geographical scopes, and thus, it is reasonable to assume that the number of threatened arthropod species was vastly underestimated in our study (Cardoso et al., 2020).

5 | CONCLUSIONS

Holm oak supports a huge number of arthropod species, thereby supporting its role as a keystone species in Mediterranean woodlands. In general, closely related species have similar feeding strategies compared with distantly related species, which supports the "taxonomic signal" hypothesis (Potapov et al., 2019). Finally, we found a moderate degree of host specificity among arthropods that feed on holm oak (ca. 20% of the species), and contrary to our expectations, we did not identify higher host specificity in the most specialized feeding groups. Overall, this study provides novel insights and offers a quantitative approach to identify keystone species important for conservation purposes, particularly in the current context of ongoing biodiversity crisis. However, further research is needed in many aspects of arthropod ecology, including the distributional ranges of species, degree of habitat specialization, population sizes and network analysis. Many arthropod species that thrive in holm oak woodlands might be at risk of extinction, and they could become extinct in the near future if the current threats to holm oak persist.

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CONFLICTS OF INTEREST

The authors confirm to not have any interest conflicts.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

All of the data and R scripts used in this study are available at Dryad (Hernández-Agüero et al., 2021): https://doi.org/10.5061/dryad.r2280gbdg

ORCID

Juan Antonio Hernández-Agüero https://orcid.org/0000-0001-6584-5774
Ildefonso Ruiz-Tapiador https://orcid.org/0000-0001-9546-5393
Luis Cayuela https://orcid.org/0000-0003-3562-2662

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BIOSKETCH

Juan Antonio Hernández-Agüero is interested on study land use changes on trophic interactions such as herbivory or bird predation, and also is interested on behavioural ecology in different groups of vertebrates and conservation biology. **Ildefonso Ruiz-Tapiador** is an expert entomologist specialized in the study of Carabid beetles, their identification, ecology and conservation. **Luis Cayuela** is interested in the effects of deforestation and habitat fragmentation on plant diversity, the spatial and temporal patterns in changes of land use, the management of Mediterranean forests: forest decay and pest management (processionary, mistletoe), patterns and causal factors of alpha and beta diversity at a regional scale, prioritization of conservation areas, community ecology and ecoinformatics.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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APPENDIX 1

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6. **Capítulo 2:** “Effects of prey colour on bird predation: an experiment in Mediterranean woodlands.”

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Autores y filiaciones:
Juan Antonio Hernández-Agüero[1], Vicente Polo[1], Miguel García[1], Diego Simón[1], Ildefonso Ruiz Tapiador[2] y Luis Cayuela[1]

1. Departamento de Biología y Geología, Física y Química Inorgánica, Universidad Rey Juan Carlos, Madrid, Spain
2. Departamento de Ingeniería Agroforestal, Universidad Politécnica de Madrid, Madrid, Spain

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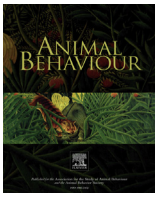

Effects of prey colour on bird predation: an experiment in Mediterranean woodlands

J. A. Hernández-Agüero [a], [*], V. Polo [a], M. García [a], D. Simón [a], I. Ruiz-Tapiador [b], L. Cayuela [a]

[a] *Departamento de Biología y Geología, Física y Química Inorgánica, Universidad Rey Juan Carlos, Madrid, Spain*
[b] *Departamento de Ingeniería Agroforestal, Universidad Politécnica de Madrid, Madrid, Spain*

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Prey detection and selection by birds can be influenced by prey coloration. Whereas certain colours can indicate to predators the unpalatability of prey (i.e. aposematism), other colours can render prey cryptic against the background. However, there are discrepancies in the response of birds to prey coloration reported in different studies. Such discrepancies can be the result of geographical or temporal (e.g. seasonal) differences between studies if birds in different regions respond differently to coloration or if responses vary seasonally due to changes in bird composition. Experimental studies aiming to understand bird responses to prey colour should consider the effect of geographical variation while accounting for seasonal as well as interannual variability. We investigated the effects of colour on attack rates by exposing plasticine caterpillars of different colours to bird communities in 13 Mediterranean forests in central Spain for a period from 17 weeks to 7 months. Overall, yellow and green dummy caterpillars suffered the lowest attack rates. We also observed a bimodal pattern of bird attack rates through time, with highest predation occurring in late winter and summer (June to September). Low attack rates on yellow dummies are probably a consequence of aposematism, while low attack rates on green dummies probably resulted from crypsis. Rapid decreases in attack rates over time are probably a result of avoidance learning, whereas the increase in attacks in summer could be explained by the increase in fledglings and migrant birds.

Predation is an important selective force in the evolution of prey coloration (Edmunds & Grayson, 1991). Coloration can be conspicuous to indicate the prey's unpalatability (i.e. aposematism) based on innate or learned colour preferences in predators. In many insects, including caterpillars, aposematism is an important antipredator strategy (Poulton, 1890; Cott, 1940). Yellow (Iniesta, Ratton, & Guerra, 2016; Lawrence & Noonan, 2018), red (Sillén-Tullberg, 1985; Svádová et al., 2009; Wennersten & Forsman, 2009), orange or different combinations of these colours (Exnerová et al., 2006; Carroll & Sherratt, 2013) have been reported as aposematic. Recently, a worldwide study found evidence of lower attack rates on yellow caterpillar versus other colours in temperate and cold but not in tropical climates (Zvereva et al., 2019). Studies with naïve birds show that many species have innate aversion to some colours in prey (i.e. unlearned avoidance, Lindström, Alatalo, & Mappes, 1999). In addition, the avoidance of certain colours may result from neophobia (Coppinger, 1970). Avoidance learning probably plays a key role in aposematism as well (Sillén-Tullberg, 1985; Lindström et al., 1999).

In addition, when their colours are more similar to those in the environment, prey become cryptic and may be harder to detect (Cott, 1940; Seymoure, Raymundo, McGraw, McMillan, & Rutowski, 2018). Some colours seem to be particularly suited to reduce prey detectability in specific environments, such as greenish colours in foliage-feeding insects (Edmunds & Grayson, 1991). However, the relative effectiveness of such cryptic coloration needs further quantification.

There seems to be disparity in the responses of birds to prey colour as reported across studies. This could be the result of either geographical or temporal differences (e.g. different studies report observations from different times of the year) in the response of bird communities to prey. Geographically, a latitudinal response gradient has been reported for prey colour preferences, where white prey suffer higher attack rates in tropical climates and brown and black prey in colder climates (Zvereva et al., 2019). Predation attack rates also seem to vary over time (Remmel, Tammaru, &

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* Correspondence: J. A. Hernández-Agüero, Departamento de Biología y Geología, Física y Química Inorgánica, Universidad Rey Juan Carlos, c/ Tulipán s/n, Móstoles, Madrid, E-28933, Spain.

E-mail address: juan.aguero@urjc.es (J. A. Hernández-Agüero).

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Maegi, 2009; Molleman, Remmel, & Sam, 2016), with higher rates of attack on caterpillars with warning coloration occurring mostly when young birds have just fledged and decreasing when naïve birds become rare (early and late in the season; Mappes, Kokko, Ojala, & Lindström, 2014). Thus, a solid understanding of the role of prey colour in bird predation requires minimizing the effect of geographical variation while accounting for temporal variability, both within (i.e. seasonal) and between years, something that has not yet been reported in the literature (but see Molleman et al. (2016) for an example of seasonal variability in attack rate on dummy caterpillars). Furthermore, while studies conducted on a global scale can provide insightful knowledge on large-scale biogeographical patterns of visual signalling (see e.g. Zvereva et al., 2019), fine-grained studies can help us understand the ecological mechanisms driving the effects of prey colour on bird predation in a particular environment.

In this study we investigated the effects of prey colour display on bird predation across bird communities living in Mediterranean vegetation woodlands. Specifically, we aimed to (1) determine whether the selection or avoidance of prey based on their colour is consistent in space and (2) quantify temporal patterns in the intensity of bird predation attacks. To achieve these goals, we placed and revisited, both throughout the year and between years, plasticine caterpillars of different colours in 13 locations in central Spain.

METHODS

Study Area

The study was conducted in 13 Mediterranean woodlands located within a 1.4° latitude range in central Spain (Fig. 1a, b). The sites were segregated into two groups, each subjected to a different experimental design. The first group (henceforth referred to as the ‘eight-colour experiment’) consisted of two sites in the Community of Madrid (Manzanares el Real and Robledo de Chavela; Fig. 1c). Both were dominated by *Quercus ilex* and *Cistus ladanifer*, but other woody species, such as *Acer monspessulanum*, were also present. Both localities had southern exposure and low disturbance by freerange cattle and humans. The second group (henceforth referred to as the ‘three-colour experiment’) consisted of 11 sites spread across a broader geographical range (Fig. 1), with *Q. ilex* also as the dominant species. The soils of the two sites of the eight-colour experiment were umbrisols and luvisols derived from gneisses and granites, whereas the soils of the three-colour experiment were mostly luvisols, regosols and leptosols. The climate in all sites was characterized by mild and rainy winters, hot and dry summers and high variability in temperature and rainfall between years (Fig. 1). The bird community composition in our study sites is given in Appendix Table A1.

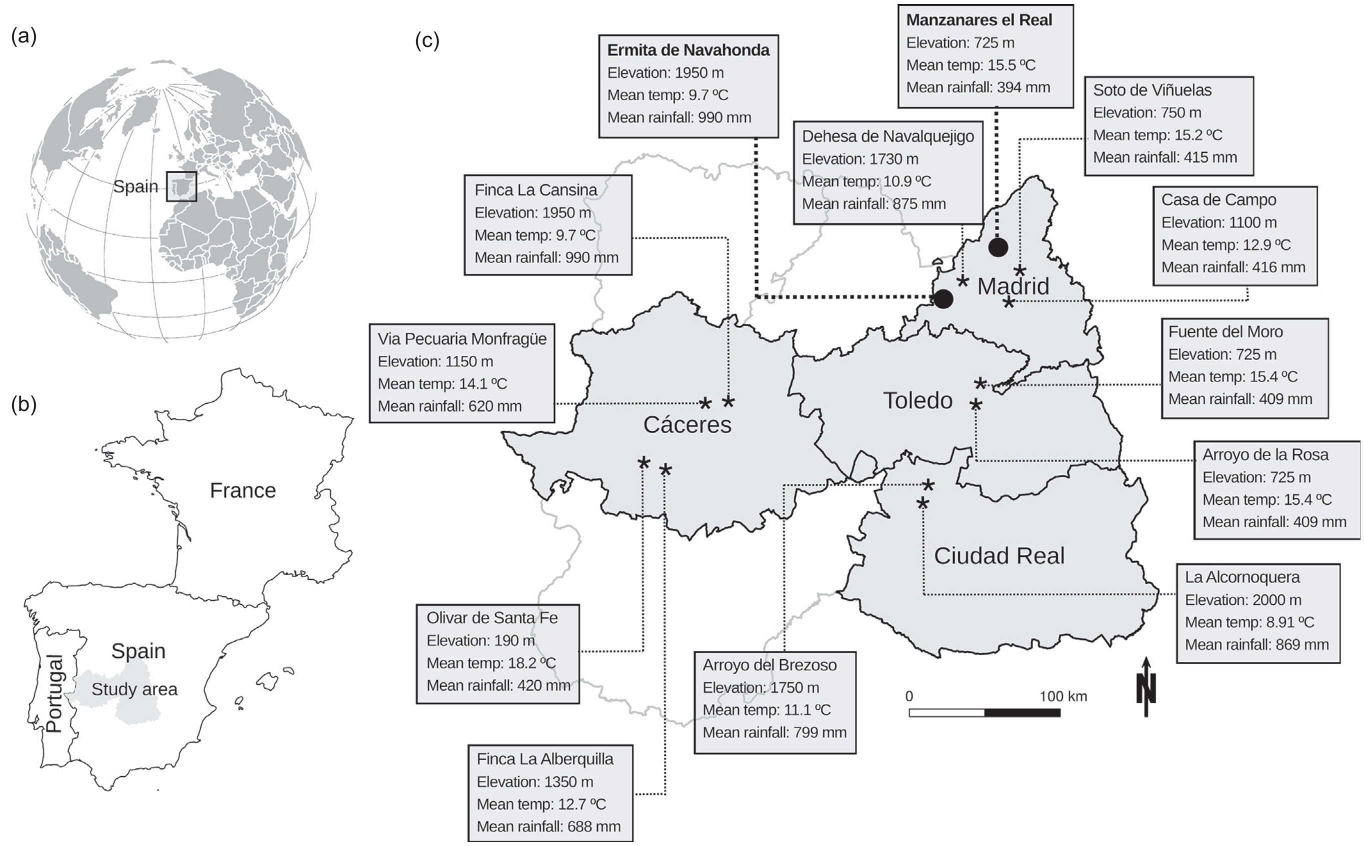

Figure 1. Distribution of the study sites: (a) location of Spain in the world; (b) location of the study area within Spain (in grey); and (c) location, elevation and mean temperature and rainfall of the two sites used for the eight-colour experiment (•), and the 11 sites used for the three-colour experiment (*). Coordinates of study sites are givenin Appendix Table A2.

Sampling Design

To determine whether birds selectively preyed on caterpillars based on their colour, we compared the number of plasticine caterpillars of different colours attacked by birds. Artificial caterpillars have been widely tested and found appropriate to investigate the effects of colour display on bird predation (Allen, Raison, & Weale, 1998; Howe, Lövei, & Nachman, 2009; Remmel & Tammaru, 2009; Iniesta et al., 2016; Molleman et al., 2016; Muiruri, Rainio, & Koricheva, 2016; Saavedra & Amo, 2018; Zvereva et al., 2019). The plasticine caterpillars were made from odourless plasticine (Chemical plant 'Luch', Yaroslavl, Russia) 30 mm long and 4 mm in diameter, with a 0.5 mm wire threaded longitudinally through each model to attach them to branches. Caterpillars were placed on thin branches (3–10 mm) at a height of 1.5–2 m, and at an average distance of ca. 30 cm from each other (but at least 20 cm apart). Dummy prey exposed 30–50 cm apart have been considered statistically independent in previous studies (Tvardikova & Novotny, 2012; Bereczki, Ódor, Csóka, Mag, & Báldi, 2014; Dattilo et al., 2016). As bird colour vision is based on four single cone types, which allows them to see in the ultraviolet range (300–700 nm; Bennett & Théry, 2007), we performed a colour analysis of the plasticine using a spectrophotometer (Jaz DPUVR Module, Ocean Optics Inc., Dunedin, FL, U.S.A.). We detected low reflectance, that is, effectiveness in reflecting radiant energy, in the UV range, with no peaks (Appendix Fig. A1).

The attack marks left on the plasticine caterpillars allowed us to identify the type of predator: bird, mammal, reptile or insect (Low, Sam, McArthur, Posa, & Hochuli, 2014). This method, however, did not allow us to attribute the damage to a particular predator species or to one or several individuals when there were two or more marks on a plasticine caterpillar (Hossie & Sherratt, 2013). For the eight-colour experiment, eight artificial caterpillars, each of a different colour (black, brown, blue, green, purple, red, white and yellow) were placed on 15 randomly selected trees and bushes (five *Q. ilex*, five *C. ladanifer* and five *A. monspessulanum*), at least 40 m apart, totalling 120 caterpillars per site. The selection of colours aimed to represent a wide variety of chromatic and achromatic (i.e. luminance) conditions (Zvereva et al., 2019). Each site was visited weekly for a 17-week period (from 8 March to 4 July 2018). This encompassed the breeding season and emergence of fledglings when bird foraging activity was probably highest.

For the three-colour experiment, three plasticine caterpillars (brown, green, yellow) were placed on five *Q. ilex* trees in each of the 11 sites, accounting for a total of 165 caterpillars in 2018 and another 165 in 2019. Each site was visited monthly for 7 months in 2018 (7 May to 10 December) and 3 months in 2019 (6 May to 26 July). Every time a locality was revisited, the number of damage marks on each caterpillar was counted and assigned to a predator type. When damage was detected, the caterpillars were repaired and moulded into their initial shape or replaced if damage was excessive or if they were lost. Following Low et al. (2014), the identification and the amount of damage were consistently recorded by three of the authors of this paper either in the field or by examining photographs. Note that the overall attack rates for the entire period from one of the localities (Ermita de Navahonda) were also used in a study of latitudinal patterns of arthropod predation (Zvereva et al., 2019).

Data analyses

To determine whether birds selectively preyed on caterpillars based on their colour, we explored the relationship between the presence or absence of damage and the colour of a caterpillar. Analyses were conducted independently for the two experiments. In all cases, we used generalized linear mixed models (GLMM) with a binomial error distribution, and presence/absence of damage as the response variable. In the eight-colour experiment, we used colour (eight levels), site (two levels), tree species (three levels) and a quadratic polynomial of the day of the year as fixed effects, including all possible interactions between colour and the other predictors. Caterpillar ID was included as a random factor to account for the autocorrelation structure of measuring damage upon the same caterpillar at different dates. In the three-colour experiment, we used colour (three levels) and a quadratic polynomial of the day of the year, as well as their interaction, as fixed effects, and site and caterpillar ID as random factors. We also include the interaction between site and colour as a random effect to specifically test whether the effect of colour on the attack probability varied between sites. The reason why site was not included as a random factor in the eight-colour experiment was that we did not have enough levels of the factor (more than five at a minimum) for reliable inference (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). Alternative models were compared using the Akaike information criterion corrected for small sample sizes (AICc). Models with a difference in AICc > 2 indicated that the worst model could be omitted. Akaike weights (w_i) were calculated for the confidence set of models (ΔAICc < 2) to determine the weight of evidence in favour of each model and to estimate the relative importance of each individual parameter in the set of candidate models. When no single model was clearly superior to the others in a set of models (model with $w_i < 0.9$), a (weighted) model averaging approach was used (Burnham & Anderson, 2002). Hence, we used the entire set of plausible models (ΔAICc < 2) to calculate model-averaged estimates for variables included in the confidence set of models and their unconditional standard errors. This approach reduces model selection bias effects on regression coefficient estimates in all selected subsets (Burnham & Anderson, 2002). Following Nakagawa and Schielzeth (2013), we estimated the R^2 of all plausible models. This allows for two components of R^2 to be calculated: (1) a marginal R^2 (R^2m) that only considers the variability explained by fixed effects; and (2) a conditional R^2 (R^2c) that accounts for the variability supported by both the fixed and random effects. Model residuals were explored using a simulation-based approach to create readily interpretable scaled (quantile) residuals for the fitted GLMMs (Hartig, 2019). When colour affected the probability of a caterpillar being attacked, multiple Tukey post hoc comparisons were conducted to determine which colours had the lowest and the highest probability of being attacked by birds. Multiple comparisons were also performed on tree species in the analyses of the eight-colour experiment data.

All analyses were performed using the R environment (version 3.5.1; R Core Team, 2019), including packages 'lme4' (Bates, Maechler, Bolker, & Walker, 2015), 'MuMIn' (Barton, 2018), 'multcomp' (Hothorn, Bretz, & Westfall, 2008), 'pavo' (Maia, Gruson, Endler, & White, 2019) and 'DHARMa' (Hartig, 2019).

Ethical Note

We did not disturb birds at all, since we observed their predatory behaviour by means of indirect evidence such as the attack marks left by predators on the artificial caterpillar. Because all localities have been historically subjected to human use (e.g. cattle ranging, hiking, bird watching), we are confident that placing artificial caterpillars in each locality had no effect on the baseline behaviour of bird communities during the breeding season. We could thus obtain information on bird predation responses without altering their behaviour and/or preferences. The plasticine used in this study was nontoxic. The set-up of predation experiments during bird breeding, including placement of artificial caterpillars, was approved by the corresponding regional environmental agencies.

RESULTS

Of the 4080 plasticine caterpillars placed for the eight-colour experiment (revisited once a week), 188 caterpillars were damaged, with 178 of the attack marks produced by birds (Table 1): 88 in the Manzanares el Real site and 90 in Ermita de Navahonda. The three best models explained with similar likelihood (with $\Delta\text{AICc} \leq 2$) the probability of a plasticine caterpillar being attacked by a bird (Table 2). All three models included the effect of tree species, the caterpillar colour and the quadratic polynomial of the day of the year, and varied in the interaction between the day of the year or its quadratic form with the caterpillar colour, and the effect of site, which was only present in one model (see Table 3 for estimated model coefficients). None of the best-fit models included the interaction between colour and tree or colour and site. Post hoc tests on both models identified two groups of colours with different rates of attack: the group with the fewest attacks included yellow, white, purple, green, blue and red caterpillars, whereas the group with the most attacks included caterpillars of any colour but yellow (Fig. 2). Post hoc tests also indicated that there were lower rates of attack on caterpillars placed on *C. ladanifer*, whereas caterpillars placed on either *A. monspesulanum* or *Q. ilex* received a similar number of attacks.

Of the 1641 caterpillars placed for the three-colour experiment (revisited approximately once a month), 921 were damaged overall, with 918 of the attack marks produced by birds (Table 1). The two best-fit models included the caterpillar colour and the quadratic polynomial of the day of the year as fixed factors and varied in the interaction between the day of the year or its quadratic form with the caterpillar colour (Table 2). Both models had the same random effects, which included the caterpillar ID and the site, but not the interaction between site and colour. Post hoc tests identified two groups of colours with different rates of attack: the one with the fewest attacks included yellow and green caterpillars, whereas the group with the most included brown caterpillars (Fig. 3).

In the eight-colour experiment, we detected a large number of damaged caterpillars at the beginning of the experiment (March), followed by a decrease during spring (April, May) and then an increase in early summer (mid-June; Fig. 2). In the three-colour experiment, there was a steady increase in the attack probability from early June throughout August, and then a decrease from October to November (Fig. 3).

DISCUSSION

The only trend seemingly consistent across sites and experiments is the lower attack rate on yellow compared to brown caterpillars. Yellow caterpillars seemed to suffer lower attack rates than black and brown caterpillars in the eight-colour experiment, whereas green suffered as few attacks as yellow caterpillars in the three-colour experiment. Despite differences in bird community composition across sites (see Appendix Table A1), the effects of prey colour on bird predation did not vary geographically, as denoted by the relatively low weight of this interaction in the set of best-fit models for the eight-colour experiment and the lack of interaction between colour and site in the three-colour experiment. This indicates that birds' response to prey colour in Mediterranean woodlands are consistent throughout space.

Colour avoidance (i.e. due to aposematism) has been noticed in previous studies (Remmel & Tammaru, 2009; Iniesta et al., 2016; Lawrence & Noonan, 2018). However, most research has focused on antipredator responses of single bird species (e.g. great tits, *Parus major*, Sillén-Tullberg, 1985; Svádová et al., 2009), laboratory experiments (e.g. Exnerová et al., 2006) and/or the study of attack rates on caterpillars displaying a combination of colours and patterns (e.g. Willmott, Elias, & Sourakov, 2011). This study broadens our understanding of wild bird community level responses to prey colour avoidance or preference. Our results are consistent with a recent worldwide study (Zvereva et al., 2019) by showing a lower attack rate on yellow caterpillars, at least for temperate and cold climates. However, we cannot exclude that colours such as blue, white or purple may be aposematic to the birds at our study sites (e.g. white: Exnerová et al., 2006, Zvereva et al., 2019 for temperate climates; blue: Zvereva et al., 2019 for cold climates; or a combination of blue and yellow: Willmott et al., 2011). Contrary to previous studies (Sillén-Tullberg, 1985; Svádová et al., 2009; Wennersten & Forsman, 2009), we did not find evidence of avoidance of red caterpillars. This result could be explained by an increase in the number of attacks in June and July (Fig. 2), a period

Table 1
Summary of the two experimental designs used to investigate the effects of prey colour on bird predation

Experimental design	No. of sites	Years	Frequency of observations	No. of observations	Total no. of caterpillars	Total no. of observations	No of bird attacks
Eight-colour	2	2018	Weekly	17	240	4077	178
Three-colour	11	2018/2019	Monthly	10	165	1641	918

Table 2
Plausible models for the attack rates of plasticine caterpillars in the two experiments

Fixed effects									Random effects					
Colour	Tree sp.	Day of the Year	Day of the Year^2	Colour * Day of the Year	Colour * Day of the Year^2	Site	Colour * Site	Colour * Tree sp.	1 | Caterpillar ID	1 | Site	Colour | Site	AICc	R^2m	R^2c
Eight-colour experiment														
	+		+	+					+	NA	NA	1433.9	0.148	0.232
+	+	+			+				+	NA	NA	1434.1	0.148	0.233
	+		+	+		+			+	NA	NA	1435.9	0.148	0.232
Three-colour experiment														
	NA	+			+	NA	NA	NA	+	+		1926.3	0.227	0.304
	NA		+	+		NA	NA	NA	+	+		1926.4	0.224	0.302

AICc: Akaike information criterion corrected for small sample sizes; R^2m: a marginal R^2 that only considers the variability explained by fixed effects; R^2c: a conditional R^2 that accounts for the variability supported by both fixed and random effects; +: fixed and random effects terms influencing the response variable in each set of models; NA: not applicable.

Table 3
Model-averaged estimates, SEs and relative importance (*wi*) for selected variables in the best-fit models

Model parameters	Estimate	SE	*wi*
Eight-colour experiment			
Fixed effects			
Intercept	3.68E+03	1.04E+03	…
Colour			
Blue	1.18E+02	8.23E+02	1.00
Brown	5.73E+02	7.07E+02	1.00
Green	−7.08E+02	8.30E+02	1.00
Purple	2.07E+02	7.48E+02	1.00
Red	−2.11E+03	1.03E+03	1.00
White	−8.38E+02	8.26E+02	1.00
Yellow	−1.43E+03	1.06E+03	1.00
Tree species			
Cistus ladanifer	2.32E+02	2.32E+02	1.00
Quercus ilex	2.05E+02	2.05E+02	1.00
Date			
Day of the Year	−1.17E+02	1.67E+01	1.00
Day of the Year^2	4.70E-01	6.62E-02	1.00
Interactions			
Blue * Day of the Year	−3.90E+00	6.51E+00	0.60
Brown * Day of the Year	−2.24E+00	5.08E+00	0.60
Green * Day of the Year	1.30E+00	5.58E+00	0.60
Purple * Day of the Year	−2.09E+00	5.36E+00	0.60
Red * Day of the Year	1.08E+01	1.04E+01	0.60
White * Day of the Year	2.99E+00	5.83E+00	0.60
Yellow * Day of the Year	1.32E+00	7.04E+00	0.60
Blue * Day of the Year^2	−9.07E-03	2.19E-02	0.40
Brown * Day of the Year^2	−3.73E-03	1.62E-02	0.40
Green * Day of the Year^2	5.31E-03	1.89E-02	0.40
Purple * Day of the Year^2	−4.25E-03	1.75E-02	0.40
Red * Day of the Year^2	2.95E-02	4.01E-02	0.40
White * Day of the Year^2	9.13E-03	2.05E-02	0.40
Yellow * Day of the Year^2	3.07E-03	2.30E-02	0.40
Site			
Manzanares el Real	−7.18E+00	7.39E+01	0.16
Random effects			
Caterpillar ID	3.60E+02		
Three-colour experiment			
Intercept	−7.08E+03	4.03E+02	…
Day			
Day of the Year	8.67E+01	2.59E+00	1.00
Day of the Year^2	−2.02E-01	5.27E-03	1.00
Colour			
Green	−2.60E+03	5.12E+02	1.00
Yellow	−2.46E+03	4.88E+02	1.00
Interaction			
Green * Day of the Year^2	1.36E-02	3.17E-03	0.51
Yellow * Day of the Year^2	1.25E-02	3.16E-03	0.51
Green * Day of the Year	6.56E+00	2.15E+00	0.49
Yellow * Day of the Year	5.99E+00	2.14E+00	0.49
Random effects			
Caterpillar ID	2.08E+02		
Site	1.60E+02		

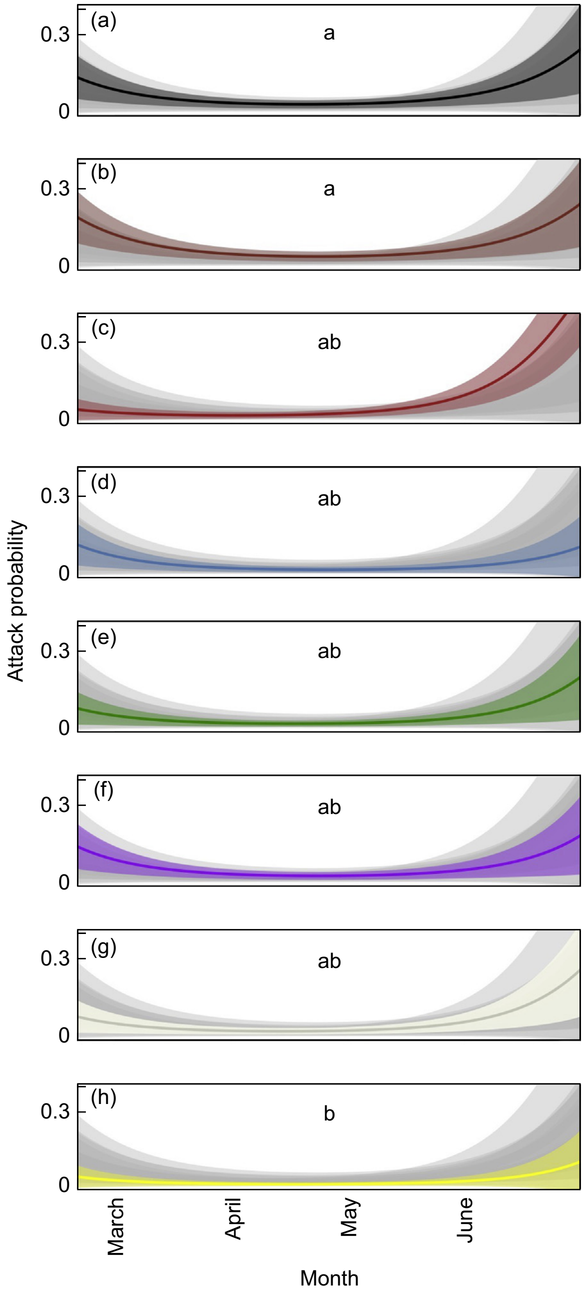

Figure 2. Model-averaged prediction plots with 95% confidence intervals for the eight-colour experiment, showing how the attack probability of a caterpillar varied through time depending on its colour. Letters represent the result of Tukey post hoc tests, with a and b indicating colours suffering statistically significant higher and lower attack rates, respectively. The colours represented are (a) black, (b) brown, (c) red, (d) blue, (e) green, (f) purple, (g) white and (h) yellow.

where many red fruits are available to birds in our study sites. The abundance of red fruits during this period might eventually trigger a functional response in birds, which would attempt to consume anything resembling a red fruit (Thompson & Willson, 1979). The disparity of results reported in the literature may be the consequence of different factors, including background colours, the presence of other colours in the prey community (e.g. Mariath, 1982; Sandoval, 1994), behavioural modifications of birds in captivity (e.g. Svádová et al., 2009), differences in light intensity (Olsson, Lind, & Kelber, 2015) or the effects of bird community composition (e.g. Nokelainen, Valkonen, Lindstedt, & Mappes, 2014), which makes it difficult to extract general conclusions.

Cryptic coloration can, additionally, result in lower attack rates. This was the case with green caterpillars in our three-colour experiment. Green caterpillars may seem a priori more palatable and thus preferentially selected by birds (Sam, Remmel, & Molleman, 2015). Being more cryptic, however, they may be harder to detect, as illustrated by the poplar hawkmoth, *Laothoe populi*, in the northwest of England (Edmunds & Grayson, 1991). The high density of plasticine caterpillars placed together within each tree in the eight-colour experiment would facilitate the detection of green caterpillars, as birds would be attracted to the microsite by more conspicuous coloured caterpillars. This then could explain why we did not see significantly fewer attacks on green caterpillars compared to other colours like we did in the three-colour experiment. The equally low attack rates on yellow and green caterpillars are in agreement with findings by Remmel

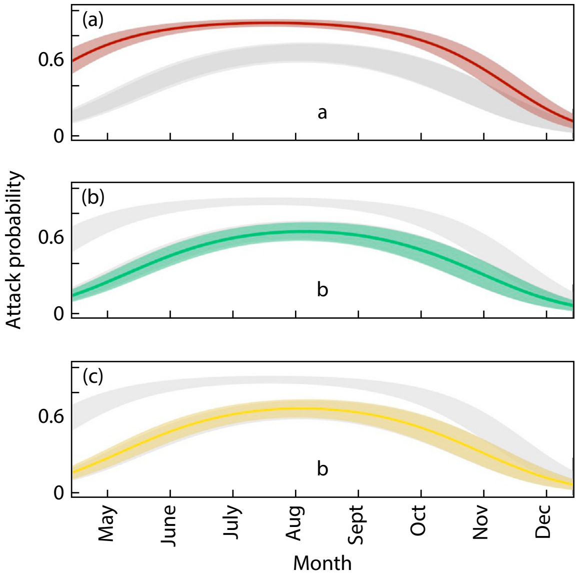

Figure 3. Model-averaged prediction plots with 95% confidence intervals for the three-colour experiment, showing how the attack probability of a caterpillar varied through time depending on its colour. Letters represent the result of Tukey post hoc tests, with a and b indicating colours suffering statistically significant higher and lower attack rates, respectively. The colours represented are (a) brown, (b) green and (c) yellow.

and Tammaru (2009): the warning signalling of aposematism may reduce attack rates as undetectability by crypsis does. However, other studies show brown to be one of the colours least predated on, possibly due to the natural crypsis of brownish caterpillars on tree bark (Mariath, 1982). The lack of consistency with our results may be a consequence of *Q. ilex* branches being more greyish than brownish, but it might also result from caterpillars being placed on thin branches (3–10 mm) within a leaf-dominated background, which possibly made them less cryptic.

A temporal pattern of attack rate was detected in both the three-colour and the eight-colour experiment. The different durations of these experiments allowed us to infer a general pattern of bimodality throughout the year. Early on (late winter in the eight-colour experiment), we observed the highest attack rates, which decreased from spring to early summer. This can be explained by birds not obtaining any reward from consuming plasticine caterpillars, so they learned to avoid preying on them. Then, in early and mid-summer (for both experiments), there was another increase in attack rates, which could be explained by the recruitment of naïve fledglings (Mappes et al., 2014). In our study areas, June is the most common month for juvenile birds to become independent and start looking for food by themselves. As fledglings become experienced, they would decrease their rate of attacks on plasticine caterpillars (late summer to autumn in the three-colour experiment). In addition, the arrival of migratory species that have no experience with the unprofitable dummies and the fact that predators leave more noticeable marks on plasticine softened by hotter conditions (Muchula, Xie, & Gurr, 2019) might contribute to explaining the maximum attack rates reached during the summer months. Consequently, the temporal pattern found in this study most probably reflects the response of birds to the characteristics of the experimental setting (i.e. reuse of dummy caterpillars over time), and little can be inferred about seasonal variability in predation rates, which might or might not follow the same pattern. Given these results, we recommend conducting experiments with plasticine caterpillars in shorter periods of time (no more than 2–3 months with monthly quantification of damage), and preferably during summer months (June to August), when predation rates are highest, to quantify predation rates at a particular time interval. Caution should be exercised when comparing predation rates between studies conducted in different seasons. In addition, we strongly recommend using independent dummy samples for each time interval, as in Molleman et al. (2016), to accurately estimate temporal variability on predation rates.

Lastly, and contrary to Sam et al. (2015), we detected lower attack rates on caterpillars placed on *C. ladanifer* compared to the other two tree species in the eight-colour experiment. It seems that *C. ladanifer* has a low abundance of prey due to the presence of flavonoids, which has a role in plant defence against herbivores (Sosa et al., 2004). A functional response to low prey abundance might therefore result in birds searching for prey less intensively in *C. ladanifer* than in the other two species.

In summary, low attack rates on yellow dummies are probably a consequence of aposematism, while low attack rates on green dummies probably resulted from crypsis. Rapid decreases in attack rates over time are probably a result of avoidance learning, whereas the increase in attacks in the warmer months could be explained by the increase in fledglings and the appearance of migrant adults.

Declaration of Interest

None declared.

Acknowledgments

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Appendix

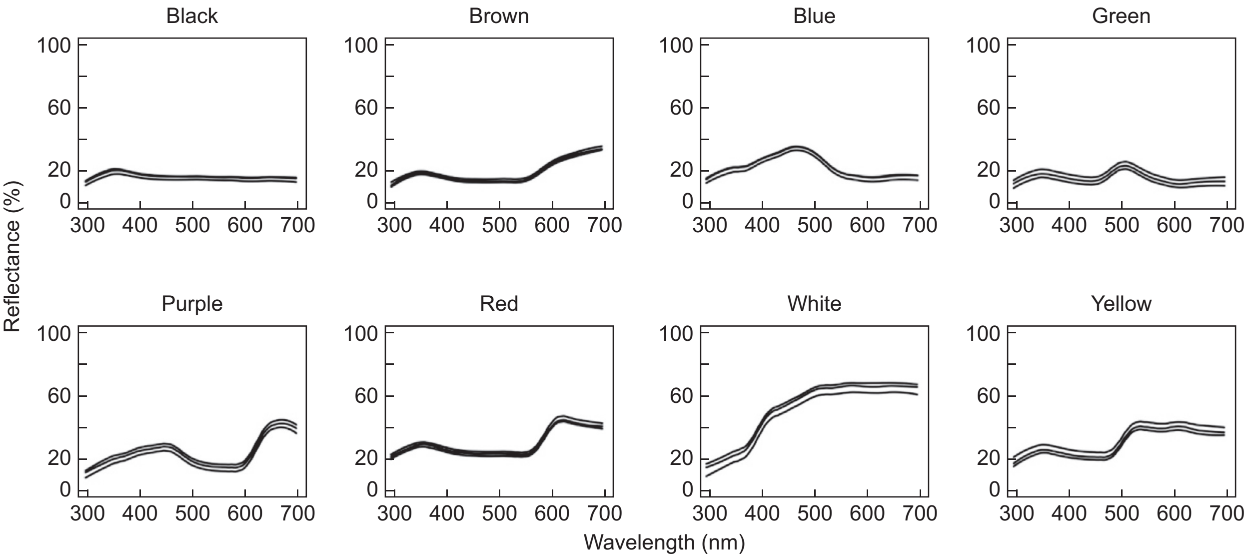

Figure A1. Reflectance (%) per wavelength (nm) of the plasticine colours used in this study.

Table A1
Bird species present in each study site based on censuses conducted during spring 2018 and 2019

Species	Feeding guild	AIT	ALC	CFA	DNF	ESP	FLC	AIT	LBC	MDV	OSF	VPM	MER	ENM
Aegithalos caudatus	Insectivorous				1	1						1	1	1
Apus apus	Insectivorous			1		1					1			
Certhia brachydactyla	Insectivorous				1					1				1
Cettia cetti	Insectivorous	1												
Coracias garrulus	Insectivorous				1									
Cuculus canorus	Insectivorous		1	1	1		1		1	1				1
Delichon urbicum	Insectivorous		1	1			1	1				1		
Dendrocopos major	Insectivorous	1			1	1		1	1					1
Ficedula hypoleuca	Insectivorous						1							
Hirundo rustica	Insectivorous	1	1			1	1	1		1	1	1		1
Lanius senator	Insectivorous		1	1			1							
Merops apiaster	Insectivorous	1	1	1	1	1		1	1	1	1	1		
Regulus ignicapilla	Insectivorous												1	1
Upupa epops	Insectivorous	1	1		1	1	1	1	1		1	1		1
Alauda arvensis	Omnivorous													1
Alectoris rufa	Omnivorous	1		1		1		1				1		1
Anas platyrhynchos	Omnivorous							1					1	
Carduelis cannabina	Omnivorous		1	1		1					1			
Cyanistes caeruleus	Omnivorous	1	1	1	1	1	1		1		1	1	1	1
Cyanopica cooki	Omnivorous			1	1		1		1	1	1		1	
Emberiza cia	Omnivorous		1				1	1			1	1		1
Erithacus rubecula	Omnivorous			1					1		1		1	1
Fringilla coelebs	Omnivorous	1	1	1	1	1	1	1	1	1	1	1	1	1
Galerida cristata	Omnivorous		1	1				1		1	1			
Galerida theklae	Omnivorous			1										
Garrulus glandarius	Omnivorous	1											1	1
Lophophanes cristatus	Omnivorous												1	1
Lullula arborea	Omnivorous						1							
Melanocorypha calandra	Omnivorous						1							
Emberiza calandra	Omnivorous		1		1									
Oenanthe oenanthe	Omnivorous		1											
Oriolus oriolus	Omnivorous	1	1		1				1				1	1
Parus major	Omnivorous	1	1	1	1	1	1	1	1	1	1	1		1
Passer domesticus	Omnivorous						1	1			1			1
Phylloscopus collybita	Omnivorous												1	
Pica pica	Omnivorous	1		1	1	1	1	1	1	1	1			1
Serinus serinus	Omnivorous							1			1	1		1

Table A1 (*continued*)

Species	Feeding guild	AIT	ALC	CFA	DNF	ESP	FLC	AIT	LBC	MDV	OSF	VPM	MER	ENM
Sitta europaea	Omnivorous					1	1		1				1	1
Sturnus unicolor	Omnivorous	1			1		1	1	1	1			1	
Sylvia atricapilla	Omnivorous	1	1	1	1	1		1	1	1	1	1	1	1
Sylvia melanocephala	Omnivorous								1					
Turdus merula	Omnivorous	1	1	1	1	1	1	1	1	1	1	1	1	1
Turdus philomelos	Omnivorous	1		1	1				1	1	1	1	1	1
Turdus viscivorus	Omnivorous						1							
Carduelis carduelis	Granivorous	1		1		1		1		1	1			1
Columba palumbus	Granivorous	1	1	1	1	1	1	1	1	1	1	1		1
Streptopelia decaocto	Granivorous		1	1	1		1	1	1	1	1	1	1	1

Censuses followed the point count method (Bibby, Burgess, Hill, & Mustoe, 2000). AIT: Arroyo de la Rosa; ALC: La Alcornoquera; CFA: Finca la Alberquilla; DNF: Dehesa de Navalquejigo; ESP: Casa de Campo; FLC: Finca la Cansina; AIT: Fuente del Moro; LBC: Arroyo el Brezoso; MDV: Monte de Viñuelas; OSF: Olivar de Santa Fe; VPM: Vía Pecuaria Monfragüe; MER: Manzanares el Real; ENM: Ermita de Navahonda.

Table A2
Province and geographical coordinates in decimal degrees (datum WGS84) of each study site

Site	Province	Longitude	Latitude
Arroyo de la Rosa	Toledo	−4.00169	39.82723
La Alcornoquera	Ciudad Real	−4.39816	39.32645
Finca la Alberquilla	Cáceres	−6.31815	39.44623
Dehesa de Navalquejigo	Madrid	−4.19128	40.47332
Casa de Campo	Madrid	−3.7555	40.42569
Finca La Cansina	Cáceres	−5.93873	39.84422
Fuente del Moro	Toledo	−3.96821	39.8552
Arroyo del Brezoso	Ciudad Real	−4.35737	39.35531
Monte de Viñuelas	Madrid	−3.67382	40.61077
Olivar de Santa Fe	Cáceres	−6.40429	39.4868
Via Pecuaria Monfragüe	Cáceres	−6.02158	39.83281
Ermita de Navahonda	Madrid	−4.24589	40.4445
Manzanares el Real	Madrid	−3.836143	40.746847

7. **Capítulo 3:** “Opposite latitudinal patterns for bird and arthropod predation revealed in experiments with differently colored artificial prey.”

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Autores y filiaciones:
Elena L. Zvereva[1], Bastien Castagneyrol[2], Tatiana Cornelissen[3], Anders Forsman[4], **Juan Antonio Hernández-Agüero[5]**, Tero Klemola[1], Lucas Paolucci[6,7,8], Vicente Polo[5], Norma Salinas[9], Kasselman Jurie Theron[10], Guorui Xu[11], Vitali Zverev[1] y Mikhail V. Kozlov[1]

1. Department of Biology, University of Turku, Turku, Finland
2. BIOGECO, INRA, Univ. Bordeaux, Cestas Cedex, France
3. Departamento de Genética, Ecologia e Evolução, Universidade Federal de Minas Gerais, Belo Horizonte, Brazil
4. Department of Biology and Environmental Science, Linnaeus University, Kalmar, Sweden
5. Departamento de Biología y Geología, Física y Química Inorgánica, Universidad Rey Juan Carlos, Madrid, Spain
6. Setor de Ecologia e Conservação, Departamento de Biologia, Universidade Federal de Lavras, Lavras, Brazil
7. Instituto de Pesquisa Ambiental da Amazônia, Brasília, Brazil
8. Departamento de Biologia Geral, Universidade Federal de Viçosa, Campus Universitário, Viçosa, Brazil
9. Instituto de Ciencias de la Naturaleza, Territorio y Energías Renovables, Pontificia Universidad Católica del Perú, Lima, Peru
10. Department of Conservation Ecology and Entomology, Stellenbosch University, Matieland, South Africa
11. CAS Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Menglun, China

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ORIGINAL RESEARCH

Opposite latitudinal patterns for bird and arthropod predation revealed in experiments with differently colored artificial prey

Elena L. Zvereva[1] | **Bastien Castagneyrol**[2] | **Tatiana Cornelissen**[3] | **Anders Forsman**[4] | **Juan Antonio Hernández-Agüero**[5] | **Tero Klemola**[1] | **Lucas Paolucci**[6,7,8] | **Vicente Polo**[5] | **Norma Salinas**[9] | **Kasselman Jurie Theron**[10] | **Guorui Xu**[11] | **Vitali Zverev**[1] | **Mikhail V. Kozlov**[1]

[1]Department of Biology, University of Turku, Turku, Finland

[2]BIOGECO, INRA, Univ. Bordeaux, Cestas Cedex, France

[3]Departamento de Genética, Ecologia e Evolução, Universidade Federal de Minas Gerais, Belo Horizonte, Brazil

[4]Department of Biology and Environmental Science, Linnaeus University, Kalmar, Sweden

[5]Department of Biology and Geology, Physics and Inorganic Chemistry, University Rey Juan Carlos, Móstoles, Spain

[6]Setor de Ecologia e Conservação, Departamento de Biologia, Universidade Federal de Lavras, Lavras, Brazil

[7]Instituto de Pesquisa Ambiental da Amazônia, Brasília, Brazil

[8]Departamento de Biologia Geral, Universidade Federal de Viçosa, Campus Universitário, Viçosa, Brazil

[9]Instituto de Ciencias de la Naturaleza, Territorio y Energías Renovables, Pontificia Universidad Católica del Perú, Lima, Peru

[10]Department of Conservation Ecology and Entomology, Stellenbosch University, Matieland, South Africa

[11]CAS Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Menglun, China

Correspondence
Elena L. Zvereva, Department of Biology, University of Turku, FI-20014 Turku, Finland.
Email: elezve@utu.fi

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Abstract

The strength of biotic interactions is generally thought to increase toward the equator, but support for this hypothesis is contradictory. We explored whether predator attacks on artificial prey of eight different colors vary among climates and whether this variation affects the detection of latitudinal patterns in predation. Bird attack rates negatively correlated with model luminance in cold and temperate environments, but not in tropical environments. Bird predation on black and on white (extremes in luminance) models demonstrated different latitudinal patterns, presumably due to differences in prey conspicuousness between habitats with different light regimes. When attacks on models of all colors were combined, arthropod predation decreased, whereas bird predation increased with increasing latitude. We conclude that selection for prey coloration may vary geographically and according to predator identity, and that the importance of different predators may show contrasting patterns, thus weakening the overall latitudinal trend in top-down control of herbivorous insects.

KEYWORDS

arthropod predators, artificial prey, avian predators, biotic interactions, color preference, latitudinal pattern, plasticine models, predation rate

1 | INTRODUCTION

Global patterns in the intensity of trophic interactions have recently become a subject of heated debate (Moles & Ollerton, 2016). Plant–herbivore interactions have received considerable attention (e.g., Kozlov, Lanta, Zverev, & Zvereva, 2015; Moles, Bonser, Poore, Wallis, & Foley, 2011; Moreira, Abdala-Roberts, Parra-Tabla, & Mooney, 2015), whereas predator–prey interactions remain less explored (Björkman, Berggren, & Bylund, 2011). Although the prevailing view seems to be that biotic interactions become more intense at lower latitudes (Adams & Zhang, 2009; Pennings & Silliman, 2005; Roslin et al., 2017; Schemske, Mittelbach, Cornell, Sobel, & Roy, 2009), many studies of both plant–herbivore (reviewed in Moles & Ollerton, 2016) and predator–prey (Lövei & Ferrante, 2017) interactions have reported no clear latitudinal pattern in the strength of these interactions. The inconsistent outcomes of these studies may partly result from the variety of methods used to estimate intensity of trophic interactions (Anstett, Nunes, Baskett, & Kotanen, 2016; Roslin et al., 2017).

To overcome the potentially distorting effects of nonuniform methods, Roslin et al. (2017) conducted a global study on geographical patterns in predator–prey interactions, based upon exposure of identical plasticine caterpillars at multiple study sites. In line with theoretical predictions (Schemske et al., 2009), the observed predation rates decreased from low to high latitudes. However, this decrease was due to changes in arthropod predation, whereas bird predation showed no statistically significant latitudinal trend (Roslin et al., 2017). The latter result seems surprising, because birds in tropical forests were estimated to consume 2.5 times more arthropod biomass (per hectare per year) when compared with birds in temperate and boreal forests, and 25 times more biomass when compared with birds in arctic tundra (Nyffeler, Sekercioglu, & Whelan, 2018). Therefore, the predation pressure that birds impose on herbivorous insects could be expected to reach its maximum in the tropics. This disagreement regarding the global pattern in bird predation, as obtained by different methods, calls for a deeper exploration of methodological sources of variability in estimates of bird predation.

In addition to the methods employed, the biological and ecological sources of variation may have contributed to the different outcomes in studies that explored latitudinal patterns in predator–prey interactions. Attack rates on model prey with the same appearance may vary among predator individuals and species, owing to differences in perception, experience, preference, and hunger level, as well as the ability of predators to recognize and discriminate prey. Predation rates also depend on many environmental characteristics, such as visual backgrounds and light conditions, which differ considerably among habitats (Endler, 1993; Ruxton, Allen, Sherratt, & Speed, 2018). In particular, prey visual appearance is subject to substantial temporal and spatial changes due to background and ambient light availability (Théry & Gomez, 2010). Therefore, variation in the illumination regime, both between and within habitats, may cause considerable differences in predation rates on the same kind of prey. For example, predation intensity on the same object can differ between illuminated and shady environments (Cheng et al., 2018; Rojas, Rautiala, & Mappes, 2014), and variations in ultraviolet light may considerably affect the search behavior of insectivorous birds (Church, Bennett, Cuthill, & Partridge, 1998).

Bird responses to prey that differ in appearance, including coloration, are influenced by previous experience (Ruxton et al., 2018). The experience of birds in a certain habitat depends on the composition of the local prey community, and particularly on the variability in coloration of local prey species, which may differ between tropical and temperate sites (Adams, Kang, & June-Wells, 2014). Great environmental variability was found to reduce the avoidance of novel foods by birds (Greenberg & Mettke-Hofman, 2001, and references therein). These results suggest that birds in tropics—the region with the highest biodiversity (Willig, Kaufman, & Stevens, 2003)—will accept a wider range of prey types, and a wider range of colors in particular, when compared with birds in other biomes.

Rates of predation on differently colored prey in natural environments may also depend on the time relative to bird's breeding season, because young naïve birds strongly differ from adult birds in their responses to a certain prey appearance (Ruxton et al., 2018; Mappes, Kokko, Ojala, & Lindström, 2014). In addition, the responses of predators to prey coloration depend on the characteristics of predator color vision, which differ considerably both between major groups of predators (arthropods, birds, mammals, and reptiles) and within these groups (Théry & Gomez, 2010). Among animals preying on insects, discrimination of colors plays major role in predatory behavior of birds (Théry & Gomez, 2010). Arthropod predators rely mostly on chemical cues in prey search and discrimination (Traniello, 1989; Zvereva & Kozlov, 2016); nevertheless, many arthropod species possess color vision (Briscoe & Chittka, 2001), and some of them use prey coloration in their foraging behavior (Taylor, Maier, Byrne, Amin, & Morehouse, 2014). We therefore suggest that the use of a set of different prey items (instead of prey of one type) would generate more robust inferences regarding variation in predation rates among different environments.

In this study, we endeavored to advance the understanding of factors shaping global latitudinal pattern in top-down control of herbivorous insects. We conducted experiments with model prey of eight different colors to test the following hypotheses: (a) Predators differentially attack prey of different colors; (b) avian and arthropod predators differ in their responses to colors of model prey; (c) the attack rates on model prey of different colors vary among sites according to the latitude and climate of the site; and (d) the overall rates of predation decrease from low to high latitudes.

2 | MATERIALS AND METHODS

2.1 | Experimental design

The experiments were conducted in 2017–2018 using a standardized method in 11 sites worldwide, from 33°57′S to 67°38′N (Figure 1), representing cold (three sites), temperate (five sites), and tropical (three sites) climates; climatic zones were distinguished based on average midsummer temperatures (Table A1 in Appendix). The study sites were selected in natural forest environments representative for each geographic zone; more details of vegetation type in each site are provided in Table A1. At each site, five mature individuals of each of the three most common woody species (15 trees in total) were haphazardly chosen for the experiment; the selected trees were situated more than 5 m apart.

Model caterpillars were made from soft modeling clay of eight colors (Figure 2) announced to be nontoxic and odorless (Chemical plant "Luch," Yaroslavl, Russia), which had been provided to each researcher participating in the experiment. Colors were selected to cover the entire spectra from short-wave to long-wave, with black and white as not colored but contrasting in luminance. Model caterpillars of a standard size (25–30 mm length and 4–5 mm diameter) were built over a wire of 0.3–0.5 mm in diameter (Figure 2). Eight caterpillars (one of each color) were attached, individually, along thin branches of each of 15 selected trees (120 caterpillars at each site). The models were placed in the outer part of the crown at a height of 1.5–2 m and not less than 20 cm apart (Figure 3a). The two first inventories were conducted at three-day intervals, whereas the following records were conducted at one- or two-week intervals, depending on the intensity of predation. The only exception was the site in Georgia (Asia), where a single record was made 10 days after the establishment of the experiment. The total duration of the experiment was 64 days, on average, and varied from 10 to 118 days (Table A1) depending on the logistic circumstances of the observer. In ten of the 11 sites, the observations were long enough to account for seasonal changes in bird predation and preferences (described, e.g., by Mappes et al., 2014). During each record, all marks found on model caterpillars were attributed to a certain group of predators according to Low, Sam, McArthur, Posa, and Hochuli (2014), and marks of each type (Figure 3b–d) were counted. The models that had damage marks were remolded or replaced if the damage was severe.

2.2 | Plasticine color analysis

A photograph of uniform clay pieces of all eight colors was taken in RAW format using a Canon 6D camera under daylight spectrum illumination with a white reflectance standard. The image was processed using Adobe Photoshop CC, and the mean camera-specific RGB component values for each piece of plasticine were recorded.

To summarize the luminance independent (chromatic) color measures, the RG and BY ratios were calculated from camera-specific RGB component values (Table A2 in Appendix), as follows: $RG = (R - G)/(R + G)$; $BY = (B - (R + G)/2)/(B + (R + G)/2)$ (Rothery, Scott, & Morrell, 2017). These ratios describe the redness versus greenness (RG) and blueness versus yellowness (BY) of each color. We also calculated the luminance (achromatic measure) of each color as $(R + G + B)/3$ (Rothery et al., 2017) and expressed it as a percentage of the maximum component value, i.e., of 255 (Figure 4). We expected multiple predator species to attack our models; consequently, we did not attempt to transform the RGB values into an avian or other animal color space.

2.3 | Statistical analysis

Attack rates (separately by birds and by arthropod predators, and by all predators combined) were calculated as the sum of all attack marks by the respective category of predators on each model for the entire observation period, divided by the total length of the observation period in days. Attacks by mammal and reptile predators were too rare (see Section 3) to conduct separate analyses.

We analyzed the effects of different factors on predator attack rates by mixed model ANOVA (SAS GLIMMIX procedure; SAS, 2009) with climate zone (cold, temperate, and tropical), site nested within climate zone, color of model and color by climate zone interaction as fixed effects, and tree species nested within each site and tree individual nested within species as random effects. We increased the accuracy of the fixed effects *F* tests by adjusting the standard errors and denominator degrees of freedom using the latest version of the method of Kenward and Roger (2009). The significance of random effects was explored by a likelihood ratio test (Stroup, 2013). To evaluate latitudinal patterns, we calculated Pearson product–moment correlation coefficients between the estimated marginal means (obtained from mixed model ANOVA described above) of site-specific attack rates on model prey of all colors together, as well as on models of two colors with most contrasting luminance (black and white).

The relative frequencies of predator attacks on models of different colors were quantified as the percentages of attacks on models of each color among the sum of attacks on models of all eight colors. The "preference" or "avoidance" was considered statistically significant if the recorded frequency of attacks differed (Fisher exact test, $p < .05$) from 0.125 (i.e., from the probability of attack expected at random). No arthropod attacks were recorded at three sites; therefore, the color-specific attack rates for arthropod predators were estimated for eight sites only.

To account for possible directional changes in the intensity of predation in the course of the experiment due to birds learning that the artificial prey offer no nutritional reward (Mäntylä et al., 2008), we calculated site-specific means of predation rates (attacks per day) for the first record (usually made after 3 days of exposure), for all other records, and for the last record separately, and compared these means by the signed-rank test.

The associations between the frequencies of attacks on models of different colors with the chromatic (RG, BY) and achromatic (luminance) characteristics of those colors were explored by calculating Pearson product–moment correlation coefficients.

3 | RESULTS

Of the 1,320 model prey exposed at the 11 sites, 531 (40.2%) were attacked at least once by birds, 366 (27.7%) by arthropods, 15 by mammals (1.1%), and 28 (2.1%) by other predators.

Across all study sites, attack rates of birds and arthropod predators based on the first record did not differ from either all other

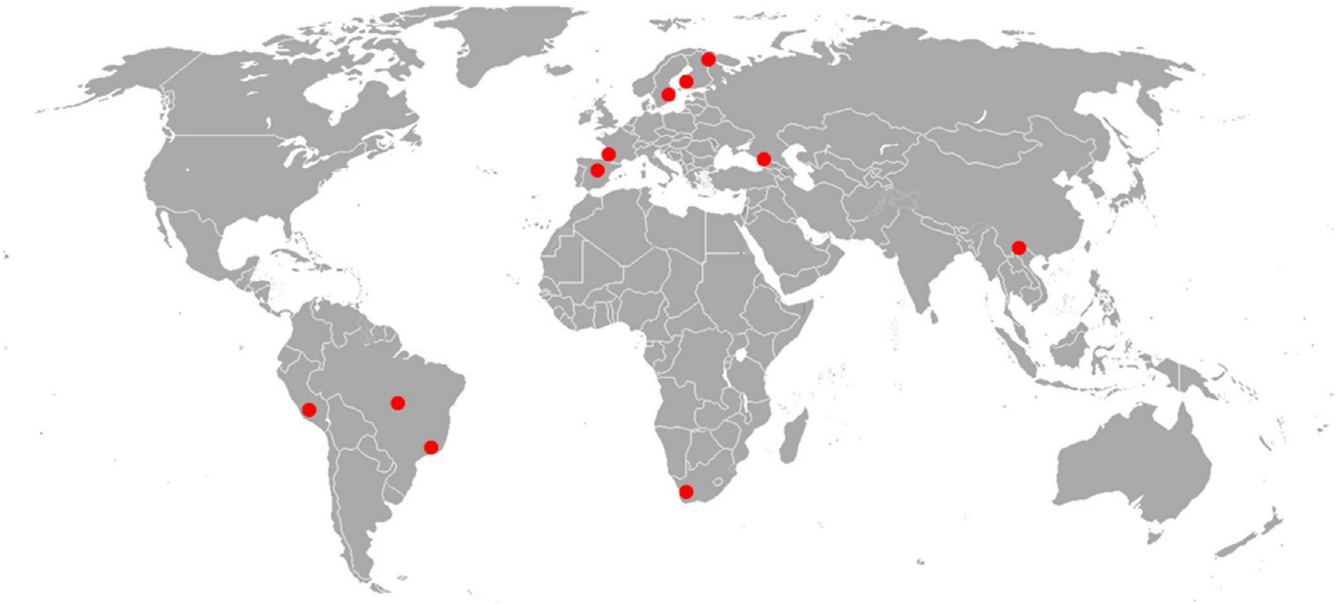

FIGURE 1 Location of the study sites. For more information, consult Table A1 in Appendix

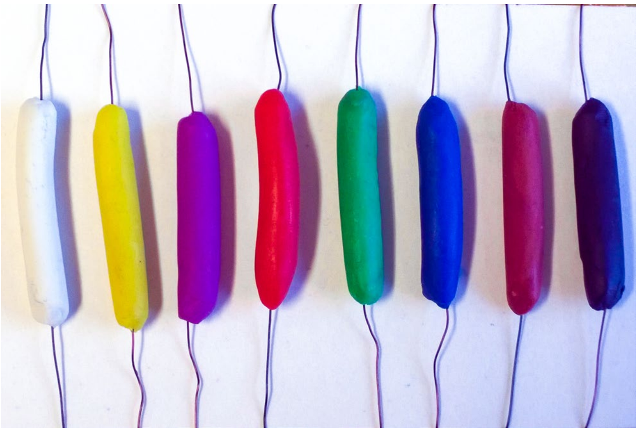

FIGURE 2 A set of plasticine caterpillars of eight different colors. This set was established on each of 15 trees per study site

records combined (*S* = 0.5, *p* = 1 and *S* = 5.5, *p* = .57, respectively) or from the very last record (*S* = 1.5, *p* = .92 and *S* = 10, *p* = .11, respectively), indicating that predators did not learn to avoid plasticine prey.

The attack rates varied among the climate zones and among the sites nested within climate zones for both avian and arthropod predators, as well as for all predators combined (Table 1). Bird predation was lowest, whereas arthropod and total predation were highest in the tropics when compared with both cold and temperate sites (Figure 5). Model color influenced bird predation rates, but did not affect arthropod predation rates (Table 1). The attack rates on models of different colors varied among the climatic zones for bird predation, but did not vary for arthropod predation (interaction terms in Table 1). The attack rates by bird and arthropod predators, as well as by all predators combined, also varied among individual trees, while the effect of tree species was marginally significant for bird predation only (Table 1).

When we compared the distributions of predator attacks among models of different colors, the proportions of predator attacks were highest on black and brown models in cold climates and on black models in temperate climates (Figure 6a,b,d,e). In tropical climates, birds disproportionally frequently attacked white models (Figure 6c), whereas arthropods attacked models of all colors (except for yellow) at similar rates (Figure 6f). Attacks on yellow models by both bird and arthropod predators were less frequent than would be expected at random in all climate zones (Figure 6a–f). The frequencies of predator attacks on models of other colors (green, blue, violet, and red) generally did not differ from those expected at random (Figure 6).

The proportions of attacks on models of different colors did not correlate with the chromatic characteristics of the models (BY and RG) neither for bird nor arthropod predators in any of the climate zones (data not shown). On the contrary, the probability of an attack on a model prey was negatively correlated with the achromatic characteristic (luminance) of the color in cold environments for both bird (*r* = −.78, *n* = 8 colors, *p* = .02) and arthropod predators (*r* = −.81, *n* = 8 colors, *p* = .02); in temperate environments for birds only (birds: *r* = −.93, *n* = 8 colors, *p* = .001; arthropods: *r* = −.26, *n* = 8 colors, *p* = .54), and was nonsignificant in tropical environments for either birds or arthropods (*r* = .24 and .24, *n* = 8 colors, *p* = .56 and .59, respectively).

The average site-specific attack rates by birds (summed across model prey of all colors for the entire observation period) increased with latitude, while the arthropod predation decreased; as a result, when the attacks by all predators were combined, the correlation between predation and latitude appeared nonsignificant (Figure 7a–c). When these correlations were calculated based on the first record only (3 days in most sites), the correlation for bird predation became nonsignificant (*r* = −.25, *n* = 11 sites, *p* = .46), whereas the correlation for arthropod predators remained marginally significant (*r* = −.58, *n* = 11 sites, *p* = .06). The bird predation rates on black and on white model prey (extremes

FIGURE 3 Examples (a) of the location of model caterpillars within a tree, five of eight colors are visible (site in Xishuangbanna, China) and of predation marks left by (b) birds, (c) arthropods, and (d) mammals

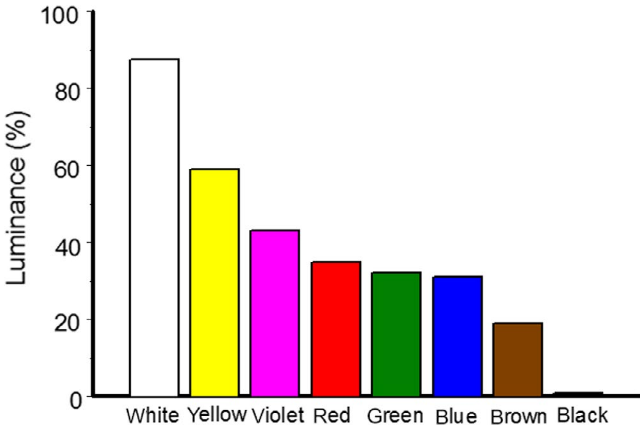

FIGURE 4 Relative luminance (percentage of the maximum component value, i.e., of 255) of eight colors of plasticine used in the experiment

in luminance) demonstrated different latitudinal patterns: The attack rates on black models significantly increased with an increase in latitude (r = .69, n = 11 sites, p = .02), whereas the attack rates on white models did not correlate with latitude (r = .08, n = 11 sites, p = .81).

4 | DISCUSSION

4.1 | Effects of model color on predator attacks

The increasing use of artificial caterpillars in ecological studies, and particularly in those studies addressing spatial patterns in predation rates (reviewed by Lövei & Ferrante, 2017), underlines the urgent need to learn how the characteristics of a model prey influence its attractiveness for predators in different environments. The exposure of differently colored model prey in multiple sites around the globe has allowed us to uncover interactive effects of environmental properties and prey color on predator attack rates.

Our finding of differential responses of birds to colors of model prey is in agreement with our expectations, because birds possess high capabilities for color discrimination, and the decisions regarding the suitability of food items made by both frugivorous and insectivorous birds greatly depend on food coloration (Théry & Gomez, 2010). However, negative correlation between probability of bird attack and prey luminance in cold and temperate climates, but not in tropical climate and, consequently, the different latitudinal trends in the frequencies of bird attacks on prey with contrasting luminance, to our knowledge, have not been reported earlier. We suggest that these discovered differential responses of birds to model luminance are associated with differences in the light regimes between the high- and low-latitude environments: In tropical forests, only 1%–5% of light transmits through the canopies, while in boreal forests it may be as high as 65% (Messier, Posada, Aubin, & Beaudet, 2009). In sparse boreal and temperate forests, a high brightness contrast between black prey and the visual background increases the probability of detection and elicits attacks by predators (Théry & Gomez, 2010). By contrast, in the shady understorey of dense tropical forests, white models showing the highest luminance were the most frequently attacked by birds. This finding is in line with the results of Cheng et al. (2018), who found that black butterfly models in tropical forests experienced lower predation

TABLE 1 Sources of variation in the attack rates on plasticine caterpillars of different colors (mixed model ANOVA, type III tests)

		Birds		Arthropod predators		All predators	
Effect	Source of variation	Test statistics	*p* value	Test statistics	*p* value	Test statistics	*p* value
Fixed	Climate zone	$F_{2,\,22} = 4.75$	.019	$F_{2,\,22} = 35.8$	<.0001	$F_{2,\,22} = 9.43$	.0011
	Color	$F_{7,\,1.134} = 2.30$	.025	$F_{7,\,1.134} = 1.89$	.07	$F_{7,\,1.134} = 3.19$	.0024
	Climate zone × Color	$F_{14,\,1.134} = 1.96$	.018	$F_{14,\,1.134} = 0.85$	.61	$F_{14,\,1.134} = 1.37$	.16
	Site (Climate zone)	$F_{8,\,22} = 3.94$	.005	$F_{8,\,22} = 2.76$	.03	$F_{8,\,22} = 2.19$	.07
Random	Tree species (Site)	$\chi^2_1 = 3.40$	.065	$\chi^2_1 = 0.00$	.98	$\chi^2_1 = 1.91$	.17
	Tree (Species × Site)	$\chi^2_1 = 7.35$	.0067	$\chi^2_1 = 21.2$	<.0001	$\chi^2_1 = 34.5$	<.0001

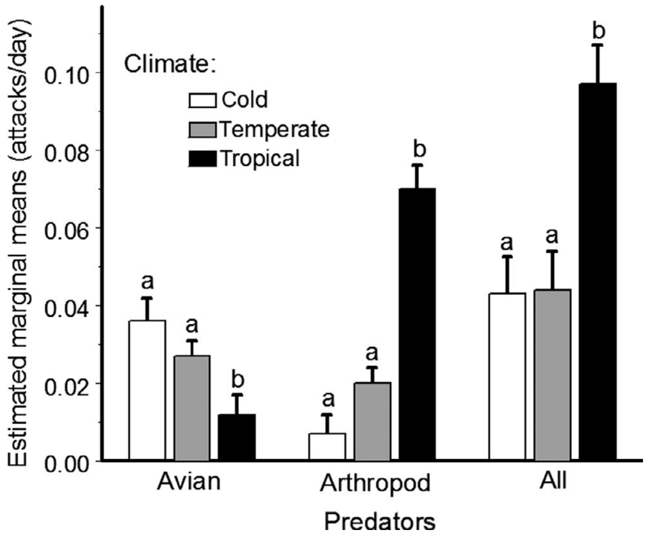

FIGURE 5 Attack rates (+ SE) of different groups of predators on plasticine models in cold, temperate, and tropical climates (all colors combined). Bars with different letters indicate significant ($p < .05$) differences between climates

rates in shady habitats than in open habitats, whereas white models showed the opposite pattern.

In our tropical sites, models of different colors were generally attacked at similar rates (except for the brightest, most attacked, white models), which may be explained by a decreased ability of birds to discriminate colors in the understory of tropical forest due to low light intensity (Gomez et al., 2014; Olsson, Lind, & Kelber, 2015). Similar attack frequencies on prey of different colors in our tropical sites might also be attributable, in part, to a higher variability in coloration of insects in the tropics, as demonstrated, for example, for butterflies (Adams et al., 2014). Birds in tropical forests are therefore faced with a higher variety of prey colors than birds in temperate and boreal forests, where models of some colors can be rejected by birds due to neophobia, that is, the avoidance of an object solely because it has never been experienced (Greenberg & Mettke-Hofman, 2001). Birds growing in diverse environments are known to exhibit decreased neophobia (Greenberg & Mettke-Hofman, 2001); therefore, birds living in tropical forests with extremely high biodiversity (Willig et al., 2003) may accept prey of a wider range of colors and patterns.

Yellow models were consistently attacked at low rates by birds across all our sites. Yellow coloration, along with other long-wavelength colors, is an effective warning signal, in particular because yellow is highly conspicuous when viewed against green foliage across a variety of habitats (Stevens & Ruxton, 2012). Birds are usually not attracted by yellow fruits (Sinnott-Armstrong et al., 2018) and avoid yellow bird feeders (Rothery et al., 2017). Interestingly, we found that yellow models were also attacked at low rates by arthropod predators in all climatic zones, indicating that yellow coloration provides effective and universal protection for prey against diverse predators in forests across a large latitudinal gradient.

Our results suggest that the strongest difference in the probability of bird attack on model prey was observed for colors that most contrasted in luminance, whereas the probability of attacks on other colors did not differ from random expectation. Taking these results together with the observed lack of correlations between prey attack rates and the chromatic characteristics of models indicates that the luminance of the prey, rather than the color itself, is the most important determinant of predation rates in environments varying in background characteristics and ambient light availability. Similarly, Cheng et al. (2018) concluded that tropical habitats that differ in light regime can have contrasting effects on prey luminance and therefore on predation risk. Luminance is especially important in the spatial vision of birds (Stevens & Cuthill, 2006), and birds generally avoid objects with high reflectance. For example, tits show an initial avoidance of glossy prey (Doktorovová et al., 2019; Waldron et al., 2017). The brightness contrast between prey and background, rather than the color contrast, may function as a warning signal also for color-blind predators (Prudic, Skemp, & Papaj, 2007).

Many invertebrate predators possess color vision (Briscoe & Chittka, 2001), and some even use prey colors in their foraging tactics (Taylor et al., 2014). However, among other cues, colors generally do not play an important role in prey detection and discrimination by arthropod predators (Zvereva & Kozlov, 2016). Ants, for example, which contribute to the vast majority of arthropod predation in the tropics (Sam, Remmel, & Molleman, 2015), primarily use chemical cues in their foraging behavior (Traniello, 1989). This explains the nonsignificant effects of prey model color on the attack rates of arthropod predators across climates. Nevertheless, in cold climates, low-luminance models (black and brown) had a higher probability of

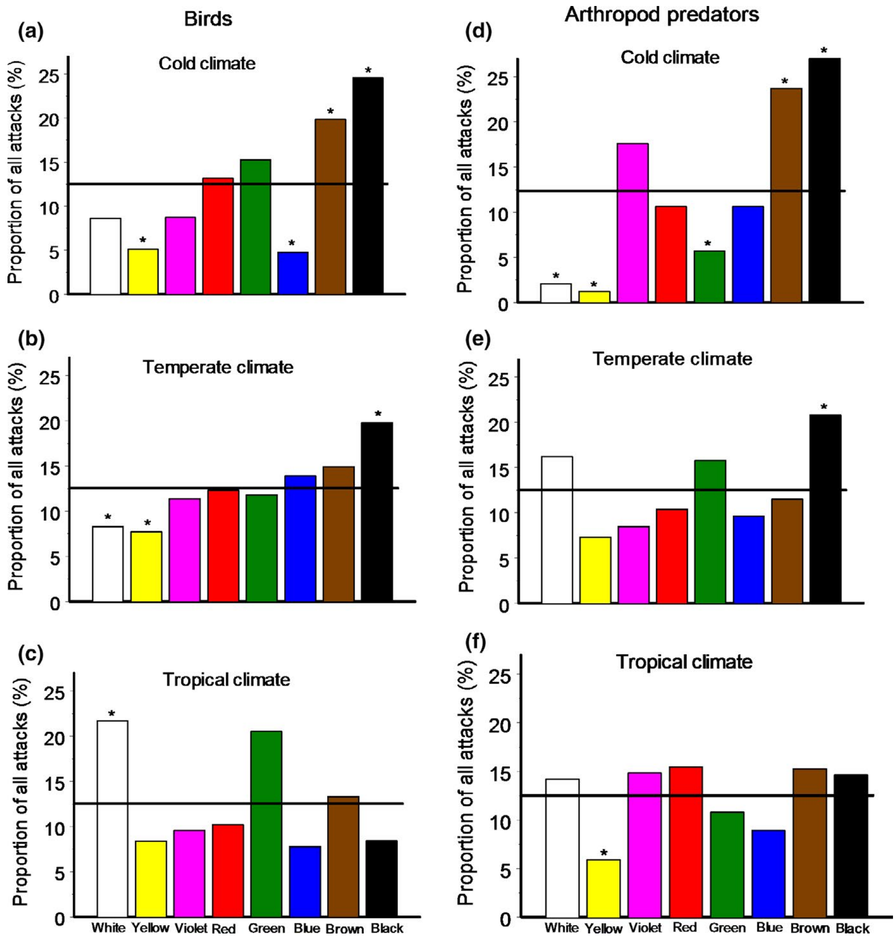

FIGURE 6 Distribution of predator attacks among different colors of model prey in different climates. Asterisks indicate significant (Fisher exact test, $p < .05$) differences from the equal probability distribution (shown by the horizontal line). Colors are ordered according to their luminance (consult Figure 4), from highest (white) to lowest (black)

arthropod predation, while high-luminance models (white and yellow) had a lower probability (Figure 4d). This indicates that the nonchromatic characteristics of coloration affect the detectability of prey not only by birds, but also by arthropod predators in high light environments, where low-luminance colors are most conspicuous. Thus, prey luminance may constitute an important factor affecting overall prey mortality.

The greater number of marks left by arthropod predators on dark models in cold climates may also reflect, in part, the effects of temperature on modeling clay. The plasticine becomes harder at low temperatures, so the visibility of arthropod predation marks decreases with decreases in ambient temperature (Muchula, Xie, & Gurr, 2019). Darker objects also heat up more rapidly in sunlight when compared with paler objects, and the difference in temperatures between black and light-colored objects increases with decreasing air temperature (Clusella Trullas, Wyk, & Spotila, 2007). Therefore, the marks of arthropod predators in cold climates may be stronger, and therefore easier to distinguish, on black and brown models than on models of colors with higher luminance.

We conclude that attack rates on model prey of different colors varied geographically and according to predator identity (Table 1, Figure 4). This supports the notion that properties of the visual background and ambient light conditions, together with differences in species composition, perceptive abilities, experiences, preferences, and demands of predators, as well as in the diversity of potential prey, can modify selection and the relative protective values of prey color patterns (Endler, 1993; Greenberg & Mettke-Hofman, 2001; Ruxton et al., 2018; Prudic et al., 2007; Wennersten & Forsman, 2009; Théry & Gomez, 2010). It remains to be investigated whether distributions of different colors across natural communities of insect larvae parallel the spatial differences in selection indicated by our results, as previously demonstrated in other systems (Karpestam, Merilaita, & Forsman, 2013).

4.2 | Variation in the intensity of predator attacks among tree species and among individual trees

We found a marginally significant variation in bird predation rates among tree species on which our models were attached. This result is in line with the studies of Muiruri, Rainio, and Koricheva (2016) and of Wennersten and Forsman (2009) and may be explained by the strong foraging preferences of insectivorous birds for certain tree species (Gabbe, Robinson, & Brawn, 2002; Holmes & Robinson, 1981). In addition, variation in canopy structure among tree species, including differences in crown density, complexity, and color, may affect both the detectability and the prey accessibility (Muiruri et al., 2016; Šipoš & Kindlmann, 2013).

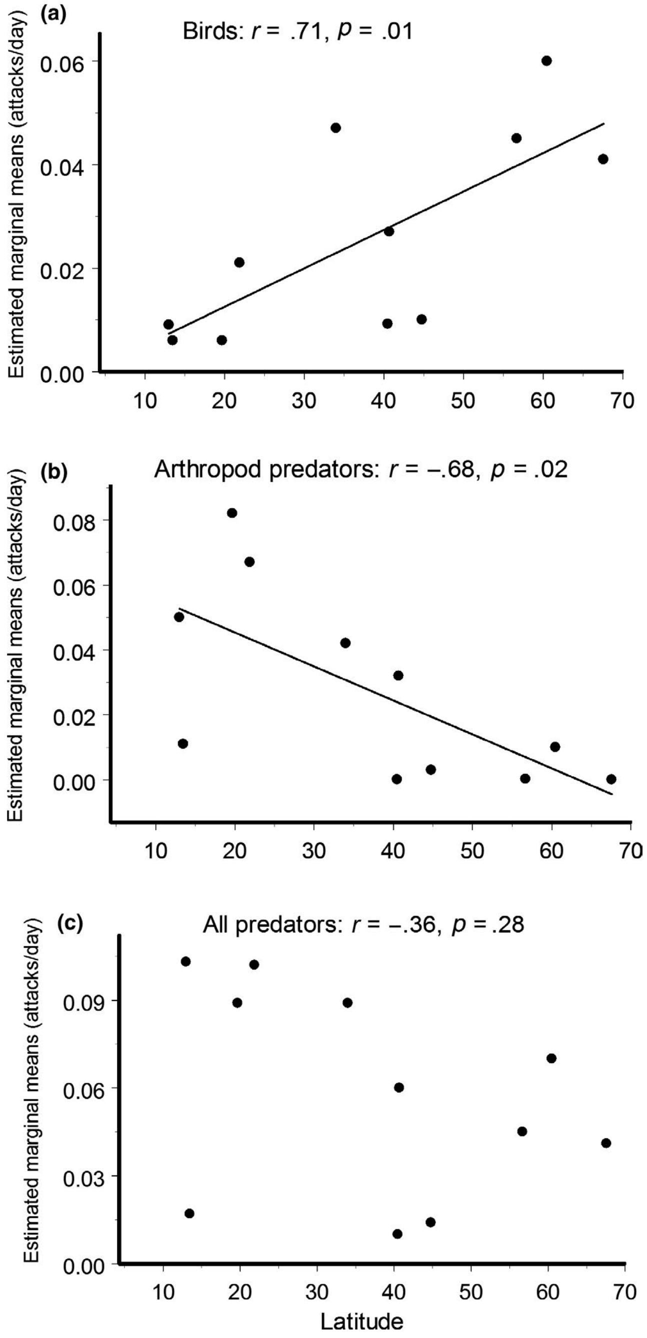

FIGURE 7 Correlation between predator attack rates (estimated marginal means; all colors summed for each tree) with the latitude of the site (a)—birds, (b)—arthropod predators, (c)—all predators (including birds, arthropods, mammals, and others)

Furthermore, both bird and arthropod predation significantly varied among individual trees, presumably due to both the obvious environmental heterogeneity of each study site and the position of a particular tree in relation to the foraging territories of predators (e.g., its nearness to bird and ant nests).

Thus, natural variation calls for the use of several plant species and considerable numbers of microhabitat replicates when conducting macroecological studies employing artificial prey.

4.3 | Geographic variation in the intensity of predator attacks

In line with the study by Roslin et al. (2017), we found that attack rates by arthropod predators on model prey decreased from low to high latitudes. The tropics are habitats with a very high abundance and diversity of arthropod predators, especially ants and wasps, which dominate the predator communities in tropical forest understoreys (Floren, Biun, & Linsenmair, 2002; Sam et al., 2015). More than a half of the studied ant species attack large caterpillars (Floren et al., 2002), and experiments with live insect prey have demonstrated higher predation rates by ants in the tropics than in temperate forests (Jeanne, 1979). Thus, the pattern revealed using plasticine caterpillars is likely to be a reliable reflection of the real latitudinal trends in arthropod predation on insect prey, which is shaped mostly by high arthropod predation in tropics.

However, a recent study showed a decreased visibility of ant attack marks when the attack took place at low temperatures (below 8°C), whereas no effect of temperature was observed on the probability of identifying visible attack marks when the attacks took place between 16 and 32°C (Muchula et al., 2019). This raised the possibility that part of arthropod predator attacks in cold climates, where temperatures during the summer season are frequently below 16°C, did not leave any visible marks on the plasticine models, thereby leading to an underestimation of arthropod predation rates at high latitudes. This potential bias may have partly contributed to the geographical pattern in arthropod predation observed in our study (Figure 6b) and in the study by Roslin et al. (2017), making the detected poleward decline steeper than it might be when investigated using natural prey.

The direction of the latitudinal gradient in bird predation rates, which we found to be lowest in tropical sites, was in strikingly contrast to our expectations. The considerably higher density of insectivorous birds and the greater biomass of arthropods consumed by birds per hectare in tropical forests relative to temperate and boreal forests (Nyffeler et al., 2018) points to the strongest bird predation pressure on herbivorous insects in tropical forests. Nevertheless, the predation rates measured using model prey demonstrate either an absence of any latitudinal trend (Roslin et al., 2017) or a significant poleward increase in bird predation (this study).

This discrepancy may be explained by several factors. First, most of the studies on spatial patterns in predation conducted to date, including our study, employed prey items placed within reach of the observer (Lövei & Ferrante, 2017), for example, below 1 m in the study by Roslin et al. (2017). This may lead to an underestimation of bird predation in tropical forests, where both bird enclosures (van Bael, Brawn, & Robinson, 2003) and model caterpillars (Loiselle & Farji-Brener, 2002) revealed higher rates of bird predation in the top canopy than in the lower forest strata. Model caterpillars placed in tropical forest understoreys sometimes showed no signs of bird predation (Sam et al., 2015). These results may be at least partly due to the higher abundance of natural prey in the top canopy than in the understorey of a tropical forest (van Bael et al., 2003; Basset et al., 2015).

Second, low bird attack rates in tropical forest understoreys may be explained by the low light intensity under the canopies of dense tropical forests, which may impair prey detectability (Gomez et al., 2014; Olsson et al., 2015). Thus, bird predation measured in the understoreys of tropical forests may be biased toward underestimation of habitat-specific values, and this bias could contribute to the latitudinal pattern observed in our study. Although experimenting in top canopies is logistically challenging, we call for more studies comparing predation pressure on herbivorous insects in top canopies and understoreys in different geographic zones to obtain a more accurate estimate of habitat-specific predation values. The understanding of changes in biotic interactions across the vertical dimension is important in explaining global biodiversity patterns, particularly those associated with environmental gradients, including disturbance, latitude, and elevation (Nakamura et al., 2017).

Despite the many potential confounding factors, a poleward increase in bird attacks on plasticine models may still reflect a real latitudinal pattern of bird predation on herbivorous insects. The densities of insectivorous birds may decrease with latitude at a lower rate than the density of potential prey. Also, a high abundance of alternative food in the tropics, such as fruits and nonherbivorous arthropods (e.g., ants and spiders; Cardoso, Pekár, Jocqué, & Coddington, 2011; Floren et al., 2002), may decrease the predation pressure upon herbivorous insects.

One possible reason why we detected a significant poleward increase in bird predation, while Roslin et al. (2017) did not find any latitudinal pattern, is that the prey exposure duration was much longer in our study than in the study by Roslin et al. (2017) (64 vs. 4 days, on average, respectively). This possibility is supported by lack of a correlation between latitude and bird predation estimates based on the first record only, when our models were exposed for only 5.4 days, on average. Considerable seasonal variations in predation rates related to the breeding season of the most abundant insectivorous birds (e.g., Mappes et al., 2014; Remmel & Tammaru, 2009) may distort geographical patterns when the start of an experiment in habitats that differ in seasonality is not adjusted precisely to a certain stage of the breeding season. Our study, in line with Muiruri et al. (2016), showed that the rates of bird attacks on plasticine models did not decrease with the time of exposure, probably because avoidance learning of prey usually develops when associated with irritating or toxic compounds, while taste of plasticine is presumably neutral. Therefore, we conclude that exposure of prey during several weeks or even several months is critical for revealing macroecological patterns in bird predation on herbivorous insects, while for arthropod predation, the duration of the experiment appeared less important than it was for bird predation.

The paramount methodological advantage of our study that allowed the detection latitudinal patterns in bird predation was the use of model prey of different colors. Our results suggest that attack rates on the prey are differently affected by prey color in different environments and that summation of attacks on prey of different colors mitigates the effects of the environment on the probability of attack on a certain prey type. Thus, we are of the opinion that our experimental design provided more realistic site-specific estimates of bird predation rates when compared to the use of prey of one color across different environments. We conclude that bird predation on herbivorous insects increases from the equator toward the poles, in an opposite direction to arthropod predation and opposite the predictions of the Latitudinal Biotic Interaction Hypothesis (Schemske et al., 2009). The contrasting latitudinal patterns found in the attack rates of bird and arthropod predators, thereby weaken the overall latitudinal trend in top-down control of herbivorous insects.

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CONFLICT OF INTEREST

None declared.

AUTHOR CONTRIBUTIONS

ELZ and MVK planned the study and wrote the first draft of the manuscript. ELZ, BC, TC, AF, JAH, LP, VP, NS, KJT, GX, VZ, and MVK performed the experiments. TK and MVK conducted statistical analyses. ELZ led the writing of the manuscript, and all authors contributed critically to the drafts and gave final approval for publication.

ORCID

Elena L. Zvereva https://orcid.org/0000-0003-2934-3421
Bastien Castagneyrol https://orcid.org/0000-0001-8795-7806
Tatiana Cornelissen https://orcid.org/0000-0002-2721-7010
Anders Forsman https://orcid.org/0000-0001-9598-7618
Tero Klemola https://orcid.org/0000-0002-8510-329X
Lucas Paolucci https://orcid.org/0000-0001-6403-5200
Norma Salinas https://orcid.org/0000-0001-9941-2109
Kasselman Jurie Theron https://orcid.org/0000-0003-0739-8720
Vitali Zverev https://orcid.org/0000-0002-8090-9235
Mikhail V. Kozlov https://orcid.org/0000-0002-9500-4244

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.tx95x69sx

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APPENDIX

TABLE A1 Basic information on field experiments performed worldwide

Site, country	Coordinates and altitude	Vegetation type	Mid-summer temperature, °C	Climate	Plant species	Start date	Finish date	Number of censuses	Responsible researcher
Sacsayhuaman, Peru	13°30′20″S, 71°58′37″W 3,550 m a.s.l.	Andean tropical forest	12.9	Cold	*Escallonia resinosa, Polylepis incana, Polylepis racemosa*	17-Jul-2018	19-Oct-2018	14	N. Salinas
Apatity, Russia	67°38′21″N, 32°45′04″E 150 m a.s.l.	Subarctic taiga forest	14.3	Cold	*Betula pubescens, Pinus sylvestris, Salix myrsinifolia*	11-Jun-2018	25-Aug-2018	3	V. Zverev, M. Kozlov
Kustavi, Finland	60°31′58″N, 21°18′08″E 10 m a.s.l.	Taiga forest	16.5	Cold	*Sorbus aucuparia, Betula pubescens, Pinus sylvestris*	28-May-2018	17-Sep-2018	9	E. Zvereva
Kalmar, Sweden	56°42′39″N, 16°22′18″E, 3 m a.s.l.	Mixed temperate forest	17.5	Temperate	*Sorbus aucuparia, Quercus robur, Betula pubescens*	24-May-2018	20-Jul-2018	8	A. Forsman
Cestas, France	44°45′14″N, 0°42′36″W, 50 m a.s.l.	Mixed broadleaved temperate forest	20.2	Temperate	*Betula pendula, Quercus robur, Castanea sativa*	23-May-2017	1-Sep-2017	10	B. Castagneyrol
Mtirala, Georgia	40°40′37″N, 41°52′23″E 300 m a.s.l.	Mountain broadleaved forest	20.7	Temperate	*Alnus glutinosa* var. *barbata, Castanea sativa, Carpinus orientalis*	19-Sep-2018	29-Sep-2018	1	V. Zverev, M. Kozlov
Stellenbosch, South Africa	33°57′27″S, 18°55′16″E 270 m a.s.l.	Renosterveld-fynbos ecotone	21.2	Temperate	*Pterocelastrus tricuspidatus, Dodonaea viscosa angustifolia, Protea nitida*	1-Nov-2018	2-Dec-2018	5	K. J. Theron
Ermita de Navahonda, Spain	40°26′40″N, 4°14′46″W 842 m.a.s.l.	Mediterranean woodlands	24.2	Temperate	*Quercus ilex, Cistus ladanifer, Acer monspessulanum*	5-Mar-2018	3-Jul-2018	17	V. Polo, J. A. Hernández -Agüero
Fazenda Tanguro, Mato Grosso, Brazil	13°04′27″S, 52°22′40″W 385 m a.s.l.	Tropical evergreen forest	25.7	Tropical	*Mabea fistulifera, Sclerolobium paniculatum, Myrcia multiflora*	3-May-2018	11-Jun-2018	6	L. Paolucci
Xishuangbanna, China	21°55′05″N, 101°16′26″E 570 m a.s.l.	Tropical rainforest	26.2	Tropical	*Meiogyne* sp., *Leea compactiflora, Drypetes salicifolia*	6-Nov-2018	16-Dec-2018	3	G. Xu
Parque Estadual do Rio Doce, Brazil	19°42′23″S, 42°34′33″W 270 m a.s.l.	Atlantic forest	26.6	Tropical	*Adenocalymma subsessifolium, Sorocea guilleminiana, Casearia selloana*	28-Sep-2017	4-Nov-2017	5	T. Cornelissen

TABLE A2 Color characteristics of plasticine used in the experiment (estimated by Adobe Photoshop CC from photographs made with Canon 6D camera)

	Component values		
Plasticine color	**Red**	**Green**	**Blue**
Black	6	6	15
Blue	0	100	136
Brown	124	24	0
Green	0	162	84
Red	206	23	39
Violet	136	49	143
White	219	214	222
Yellow	212	194	48

8. **Capítulo 4:** “Latitude determines the direction of trophic interactions in response to urbanization.”

En preparación.

Autores y filiaciones:

Juan Antonio Hernández-Agüero[1], Ildefonso Ruiz-Tapiador[2], Lucas, A. Garibaldi[3,4], Mikhail V. Kozlov[5], Elina Mäntylä[6], Marcos E. Nacif[3,4], Norma Salinas[7], Vitali Zverev[5], Elena L. Zvereva[5] y Luis Cayuela[1]

1. Department of Biology and Geology, Physics and Inorganic Chemistry, Universidad Rey Juan Carlos, c/ Tulipán s/n, E28933 Móstoles,Madrid, Spain.
2. Departamento de Ingeniería Agroforestal, Universidad Politécnica de Madrid, Ciudad Universitaria s/n, E-28040 Madrid, Spain.
3. Universidad Nacional de Río Negro, Instituto de Investigaciones en Recursos Naturales, Agroecología y Desarrollo Rural, San Carlos de Bariloche, Río Negro, Argentina.
4. Consejo Nacional de Investigaciones Científicas y Técnicas, Instituto de Investigaciones en Recursos Naturales, Agroecología y Desarrollo Rural, San Carlos de Bariloche, Río Negro, Argentina.
5. Department of Biology, University of Turku, FI-20014, Turku, Finland.
6. Institute of Entomology, Biology Centre of the Czech Academy of Sciences, Ceske Budejovice, Czech Republic AND Faculty of Science, University of South Bohemia, Ceske Budejovice, Czech Republic
7. Institute for the Sciences of Nature, Territory and Renewable Energies, Pontifical Catholic University of Peru, Lima, Peru

Latitude determines the direction of trophic interactions in response to urbanization

Juan A. Hernández-Agüero[1], Ildefonso Ruiz-Tapiador[2], Lucas, A. Garibaldi[3,4], Mikhail V. Kozlov[5], Elina Mäntylä[6], Marcos E. Nacif[3,4], Norma Salinas[7], Vitali Zverev[5], Elena L. Zvereva[5] & Luis Cayuela[1]

1 Department of Biology and Geology, Physics and Inorganic Chemistry, Universidad Rey Juan Carlos, c/ Tulipán s/n, E28933 Móstoles, Madrid, Spain.
2 Departamento de Ingeniería Agroforestal, Universidad Politécnica de Madrid, Ciudad Universitaria s/n, E-28040 Madrid, Spain.
3 Universidad Nacional de Río Negro, Instituto de Investigaciones en Recursos Naturales, Agroecología y Desarrollo Rural, San Carlos de Bariloche, Río Negro, Argentina.
4 Consejo Nacional de Investigaciones Científicas y Técnicas, Instituto de Investigaciones en Recursos Naturales, Agroecología y Desarrollo Rural, San Carlos de Bariloche, Río Negro, Argentina.
5 Department of Biology, University of Turku, FI-20014, Turku, Finland.
6 Institute of Entomology, Biology Centre of the Czech Academy of Sciences, Ceske Budejovice, Czech Republic AND Faculty of Science, University of South Bohemia, Ceske Budejovice, Czech Republic
7 Institute for the Sciences of Nature, Territory and Renewable Energies, Pontifical Catholic University of Peru, Lima, Peru.

Abstract

Interactions between different trophic levels, such as plants, herbivores, and predators play an important role in ecosystem functioning. Trophic interactions can be affected by urbanization, which is currently one of the main drivers of biodiversity decline. Studies conducted at a global scale are necessary to extract generalized conclusions on the effect of urbanization on trophic interactions and determine whether these effects change along latitudinal gradients. Biotic interactions are usually more intense at lower latitudes and therefore are more likely to experience more strikingly the effects of human impacts. Here, we test the hypothesis that the impacts of urbanization on trophic interactions, specifically insect herbivory and bird predation, will decrease with latitude. To achieve this, we compiled data on insect herbivory and bird predation from different studies around the world using similar methodologies and fitted generalized linear mixed models to test the effect of human population density and latitude on these two response variables. An opposite latitudinal response patterns to urbanization was obtained, with decreases of the intensity of herbivory and predation with the increase of human population density only at lower latitudes, no changes at intermediate latitudes, and increases at higher latitudes. We explain these latitudinal differences due to the urban heat island effect that allows higher rates of trophic interactions at higher latitudes, especially in ectotherm species, compared to non-urban areas, but lower rates at lower latitudes. Cities currently act as live simulators of climate change, representing the temperature that will be experienced at the same latitude in the future. Our results can be used to assess the impact of global warming on trophic interactions at different latitudes.

Introduction

Among the many human activities that cause habitat loss, urban development produces some of the most significant local extinction rates (McKinney, 2002). At present 54% of the world population live in cities (≥ 300,000 inhabitants) and this percentage is expected to increase up to 70% by 2050 (United Nations, 2018). Cities have recurrent air and water pollution problems and cause profound changes in ecosystems, land use, biogeochemical cycles, and climate (Bai *et al.*, 2017). Such impacts produce a decline in the abundance and diversity of several species, including bats (Russo & Ancilloto, 2015), birds (Clergeau *et al.*, 1998; Gagné & Fahrig, 2011; Narango *et al.*, 2018; Planillo *et al.*, 2021), fungi (Abrego *et al.*, 2020), beetles (Gagné & Fahrig, 2011), bees (Fortel *et al.*, 2014) and other insects either terrestrial or aquatic (Hallmann *et al.*, 2017; Seibold *et al.*, 2019; Piano *et al.*, 2020; Planillo *et al.*, 2021; Boyes *et al.*, 2021).

Shifts in species composition and diversity driven by urbanization can also affect species interactions. Among all different species interactions, trophic interactions are relevant for biological communities and are responsible for essential ecosystem services, such as nutrient cycling (DeAngelis, 2012) or pest control (Whelan *et al.*, 2008). According to Gray's increasing disturbance hypothesis (Gray, 1989), urbanization can negatively affect the intensity of trophic interactions. There is evidence that urbanization can negatively affect herbivory (Miles *et al.*, 2019). Urbanization has been shown to significantly reduce herbivory in 11 woody plants species in Europe (Kozlov *et al.*, 2017), such as *Quercus robur* in Europe (Moreira *et al.*, 2019), and *Carya ovata*, *Quercus bicolor*, *Desmodium canadense* and *Vaccinium angustifolium* in New England (USA) (Meineke *et al.*, 2019). Also, there is evidence that urbanization can negatively affect predation. This situation has been exemplified by the reduction of aphid predators in response to urbanization in south England (Rocha & Fellowes, 2018), the decrease of nest predation by egg predators in urban environments in either northern (Gering & Blair, 1999) or southern USA (Thorington & Bowman, 2003) and Finland (Jokimäki & Huhta, 2000), or the decrease in bird predation from old-growth forests to fragments with higher land use intensity in Denmark (Ferrante *et al.*, 2014) and Madagascar (Schwab *et al.*, 2020). Recently, a meta-analysis made with data mainly from North America and Europe showed a decrease in bird predation with increasing urbanization (Eötvös *et al.*, 2018).

Despite widespread support for Gray's increasing disturbance hypothesis, some studies have also reported a positive effect of urbanization on herbivory in different parts of the world, including Brazil (Cuevas-Reyes *et al.*, 2013; Rivkin & Moura, 2020), Australia (Christie & Hochuli, 2005) and USA (Cregg & Dix, 2001; Dale & Frank, 2017). Likewise, attacks on caterpillars, made mainly by birds and arthropods, increased across a disturbance gradient from closed-canopy forest to rural areas in Philippines (Posa *et al.*, 2007).

These studies conducted at regional or local scales illustrate well how both herbivory and predation are context-dependent and can vary across regions. This could be explained in the light of the latitudinal gradient, with biotic interactions becoming more intense at lower latitudes (MacArthur, 1969; Schemske *et al.*, 2009), and therefore suffering more strikingly the effects of human impacts. However, the literature has contradictory evidence about the effect of the latitudinal gradient on the intensity of biotic interactions. In the particular case of herbivory, some studies point out to an increase in insect herbivory with latitude (Adams & Zhang, 2009; Del-Val & Armesto, 2010), while others report the opposite pattern (Pennings & Sillman, 2005; Pennings *et al.*, 2009; Garibaldi *et al.*, 2011; Moreira *et al.*, 2015), no latitudinal differences (Salazar & Marquis, 2012) or a peak at intermediate latitudes (Kozlov *et al.*, 2015). In the case of predation, Lövei & Ferrante (2017) found no effects of latitude on the strength of biotic interactions, whereas other studies found different and even opposite effects depending on the predator (Roslin *et al.*, 2017; Zvereva *et al.*, 2019). Such discrepancies might reconcile in the view of the urbanization effect on trophic interactions. Thus, similarly to what has been demonstrated for ecosystem functioning (Kim, 1992), the latitudinal change of trophic interactions might vary across urban gradients since there is a change in environmental conditions in urban areas compared to natural areas at the same latitude.

Studies conducted at a global scale are necessary to extract generalized conclusions about the effect of urbanization on trophic interactions and determine how these effects change along the latitudinal gradients. To date, only a few studies have tested the interaction between latitude and urbanization on trophic interactions, with none involving latitudinal gradients larger than 10° to 20° (Kozlov *et al.*, 2017; Meineke *et al.*, 2019; Moreira *et al.*, 2019). The results of such studies suggest that the effect of urbanization on herbivory remains constant along the latitudinal gradient, yet these conclusions might be hindered by the lack of broad latitudinal gradients. This study investigated the effects of human density -as a subrogate of human impact- on tri-trophic interactions (insect herbivory and bird predation) along latitudinal gradients. To achieve this goal, we compiled data on both plant-herbivore and prey-predator interactions worldwide using similar (and thus comparable) sampling procedures. Using a broad latitudinal gradient encompassing both hemispheres, we will be able to identify whether the effects of human pressure on trophic interactions are universal or change latitudinally. We expect trophic interactions to decrease in response to urbanization, with higher impacts of urbanization at lower latitudes. To our knowledge, this is the first study exploring the effects of human pressure on trophic interactions at a global scale.

Methods

We integrated: (1) data available in Kozlov *et al.* (2015), Mendes *et al.* (2021) and Hernández-Agüero *et al.* (in prep.) to investigate the effects of human population on insect herbivory (Figure 1a).; and (2) those from Mäntylä *et al.* (2008), Mäntylä *et al.* (2014), Maas *et al.* (2015), Roslin *et al.* (2017), Zvereva *et al.* (2019), Murray *et al.* (2020), Schwab *et al.* (2020), Zvereva *et* *al.* (2020), Valdés-Correcher *et al.* (2021), Gomes *et al.* (2021), Leuenberger *et al.* (2021) and Hernández-Agüero *et al.* (in prep.) to investigate the effects of human population on bird predation (Figure 1b).

Herbivory

Insect herbivory was estimated for every locality, year and tree species as the percentage of leaf area consumed by insects. The sampling methodologies used to estimate percentage of leaf area consumed by insects in Kozlov *et al.* (2015), Mendes *et al.* (2021) and Hernández-Agüero *et al.* (in prep.) were similar. They all estimated the percentage of leaf eaten either directly with image software (ImageJ) or following the methodology proposed by Alliende (1989). Herbivory data were grouped by species, year and study site as in Kozlov *et al.* (2015). Since Mendes *et al.* (2021) only provides information on the percentage of leaf eaten by chewer insects, no information about herbivory by leaf gallers or miners was used in this study. The dataset used included observations spanning from 1961 to 2020.

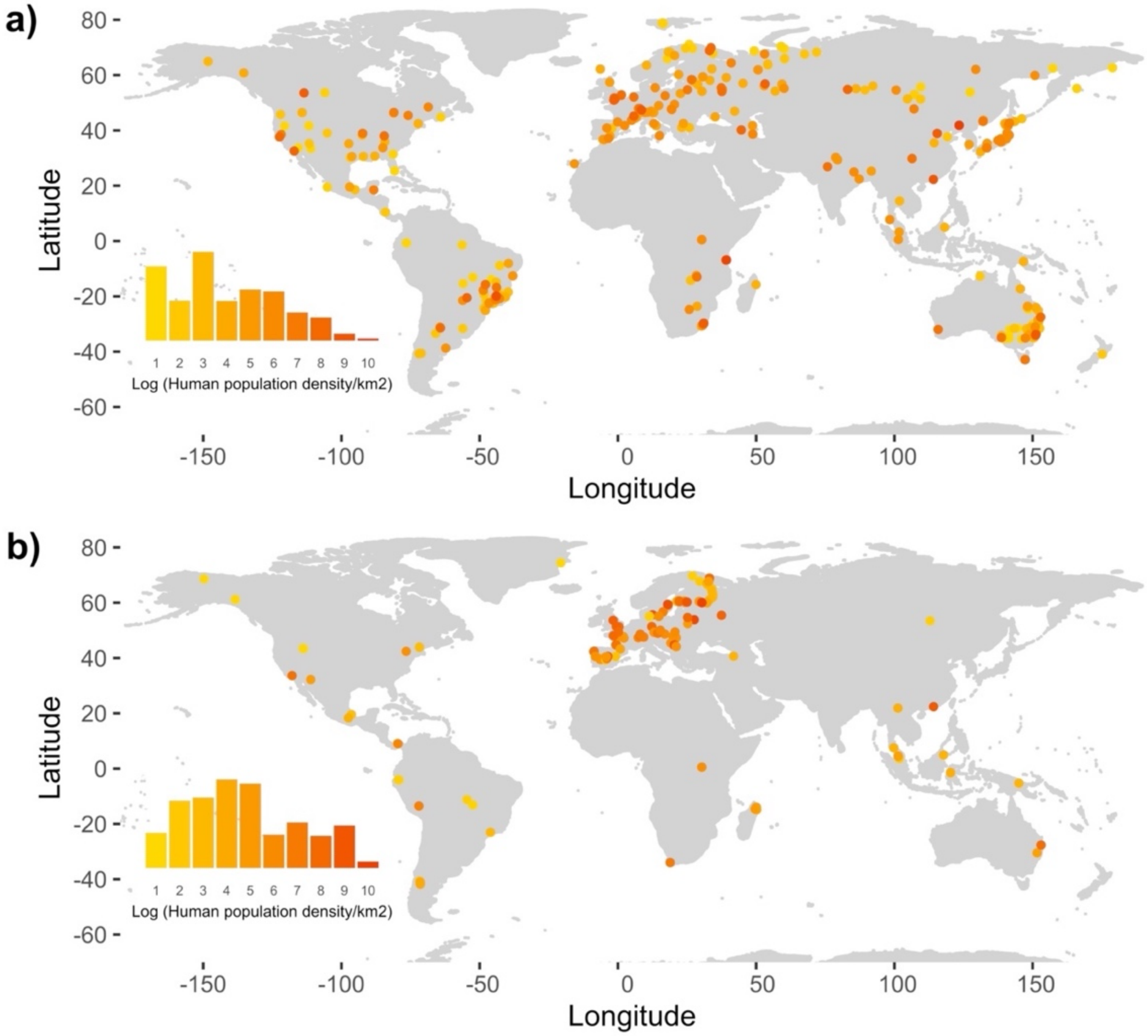

Figure 1. Location of field samples from different studies conducted across the world for a) herbivory and b) predation data, with a yellow-red scale representing the logarithm of the human population density. The frequency of every value of human population is represented in the histogram located on the bottom left of each figure.

Predation

Predation pressure by birds was estimated using artificial green caterpillars. Artificial caterpillars have been widely tested and found appropriate to investigate bird predation (Remmel & Tammaru, 2009; Low *et al.*, 2014; Zvereva *et al.*, 2019; Hernández-Agüero *et al.*, 2020). In all these studies, artificial caterpillars made of odourless plasticine of different colours (red, brown, green, purple, brown, yellow, black or white) were placed on a woody plant branch or leave, either with metal wire or glue, usually during the breeding period of local birds. Most of the studies included caterpillars of different colours, but some were based only on green-coloured caterpillars. Because colours can influence attack rates (Remmel & Tammaru, 2009; Hernández-Agüero *et al.*, 2020) and colour preferences by birds can change latitudinally, we selected only green caterpillar data, which does not show a relevant change pattern along latitudinal gradients (Zvereva *et al.*, 2019), for this study. The size of this moulded plasticine ranged from 1.5 to 3.5 cm length and 3 to 5 mm diameter. After some time (from 2 to 64 days depending on the study), the caterpillars were revisited and bird marks were counted following the methodology proposed in Low *et al.* (2014). We excluded data provided by non-scientific personnel in Valdés-Correcher *et al.* (2021) to ensure the highest data quality. The dataset used includes observations spanning from 2007 to 2020. To account for differences across studies in the length of the study period, we estimated the probability of a larvae to be attacked over one day (hencefort probability of bird predation) as:

$$P(X \geq 1) = 1 - P(X = 0) = 1 - \left[1 - \left(\frac{N}{T}\right)\right]^{\left(\frac{1}{t}\right)}$$

where $P(X \geq 1)$ is the probability of having one or more larvae attacked by birds, *N* is the number of attacked caterpillars, *T* is the total number of caterpillars used per period, and *t* is the period length in days.

Human population

We used the Gridded Population of the World (GPWv4) dataset to estimate human population density at each study site. To do so, we created a 10 km radius buffer at each locality with the 'st_buffer' function of the R package 'sf' (Pebesma, 2018). This size allowed us to characterize the surrounding areas of the study sites considering the resolution of the GPWv4 (~1 km). We then cropped the rasterized GPWv4 dataset with our locality buffer of 10 km using the 'crop' function of the R package 'raster' (Hijmans, 2020) and created a new raster object using our buffered coordinates and the GPWv4 cropped dataset with the 'mask' function. Finally, we extracted the total human population at every locality with the 'extract' function.

Data analyses

We used generalized linear mixed models (GLMM) with a beta error distribution and a logit link function to investigate the effects of human population and latitude on predation pressure by birds and insect herbivory. Beta is a family of continuous probability distributions defined on the interval [0,1], and therefore appropriate for the type of response variables we are modelling in this study. We used the logarithm of human population and absolute latitude as predictors. In the GLMMs for herbivory, we identified the following random factors: i) locality, which accounted for potential spatial autocorrelation, since we had from 1 to 49 data per location; and ii) plant species nested within genus, which accounted for differences in palatability and plant defences against herbivory among plant species. In the GLMMs for predation pressure by birds, only locality was included as a random factor to account for potential spatial autocorrelation, since we had from 1 to 12 data per location. All GLMMs were fitted using maximum likelihood with the function 'mixed_model' of the R package 'glmmTMB' (Brooks *et al.*, 2017).

For both herbivory and predation, alternative models were compared using the Akaike information criterion corrected for small sample sizes (AICc). Models with a difference in AICc > 2 indicated that the worst model could be omitted. Following Nakagawa & Schielzeth (2013), we estimated the R^2 of all plausible models. This allows for two components of R^2 to be calculated: (1) a marginal R2 (R2m) that only considers the variability explained by fixed effects; and (2) a conditional R^2 (R^2c) that accounts for the variability supported by both the fixed and random effects. Model residuals were explored using a simulation-based approach to create readily interpretable scaled (quantile) residuals for the fitted GLMMs (Hartig, 2019). Moran's index was used to estimate spatial autocorrelation in model residuals both for proportion of herbivory and probability of predation. To test for significance of spatial autocorrelation this index was compared with a null model random distribution using the R package 'spdep' (Bivand & Wong, 2018).

Results

Herbivory

We combined information on herbivory from 543 woody plant species of 281 genus in 315 different localities spanning 121.84° latitude (from -42.92° to 78.94°), with human population density ranging from 0 to 14,960 inhabitants/km^2. The mean proportion of herbivory was 0.0574 ± 0.0531. The best model to explain the variability observed in herbivory included the logarithm of the human population, absolute latitude and their interaction (Table 1). Model predictions showed differential effects of the human population on the proportion of herbivory along the latitudinal gradient. For equatorial localities, there was a decrease in herbivory as human population increases. As with predation, this effect was diluting towards more temperate latitudes and reversing at boreal latitudes, i.e. more herbivory in higher populated areas (Figure 2).

Table 1: Comparison of alternative models using the Akaike information criterion corrected for small sample sizes (AICc). The best model (lowest AICc) is indicated in boldface type. R^{2}m: a marginal R^2 that only considers the variability explained by fixed effects; R^{2}c: conditional R^2 that accounts for the variability supported by both fixed and random effects.

	Model			Bird predation	Insect herbivory		
	Predictors	**AICc**	**ΔAIC**	**R^{2}m/ R^{2}c**	**AICc**	**ΔAIC**	**R^{2}m/ R^{2}c**
AIC Fixed factors	Log (Human Population) * Abs (Latitude)	**-5472.24**		**0.033/0.14**	**-3396.69**		**0.101/ 0.675**
	Log (Human Population) + Abs (Latitude)	-5466.63	5.61		-3390.15	6.54	
	Abs (Latitude)	-5462.16	10.08		-3390.88	5.81	
	Log (Human Population)	-5449.58	22.66		-3375.89	20.8	
	Null model	-5448.57	23.67		-3376.36	20.3	

Predation

We combined information from 366 different localities spanning 116.24° latitude (from -41.78° to 74.47°), with human population density ranging from 0 to 12,869 inhabitants/km^2. The mean probability of larvae being attacked over one day was 0.0476 +/- 0.1136. As with herbivory, there was an effect of the logarithm of human population and latitude, as well as their interaction, on the probability of bird predation (Table 1). Model predictions showed changes in the effects of human population on the probability of bird predation along the latitudinal gradient. For equatorial localities there was a strong decrease on predation as human population increases. This effect was diluting towards higher latitudes (subtropical and temperate ecosystems) and reversing in boreal latitudes, i.e. more predation in higher populated areas (Figure 3).

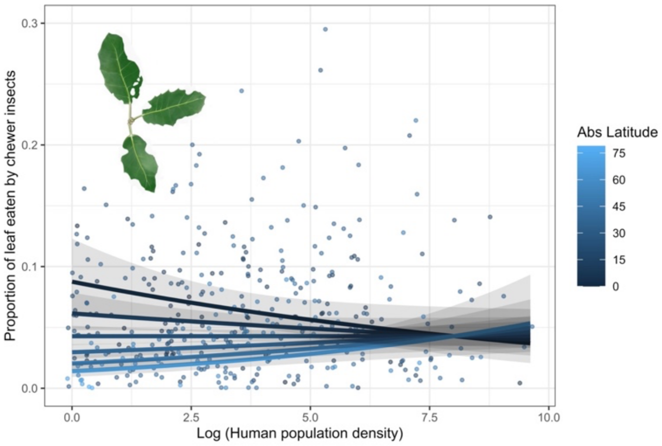

Figure 2: Predictions of generalized linear mixed models showing the proportion of herbivory with 95% confidence intervals along a gradient of human population (in logarithm) at six different latitudes. Mean observed values of the proportion of herbivory per species and locality are represented as dots. Drawing of leaves with herbivory by I. M. Alonso-Crespo.

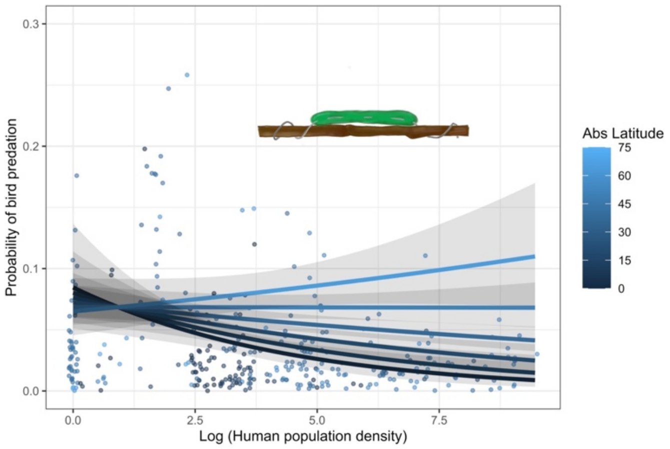

Figure 3: Predictions of generalized linear mixed models showing the probability of bird predation on green caterpillars with 95% confidence intervals along a gradient of human population (in logarithm) at six different latitudes. Mean observed values of the probability of bird predation per locality are represented as dots. Drawing of green caterpillar by I. M. Alonso-Crespo.

Discussion

We expected to find a negative impact of human population on both herbivory and predation, with this effect being more prominent at warmer equatorial latitudes. Our results confirm our initial expectations but reveal that the negative effect that urbanization has on trophic interactions intensity can turn out positive at higher latitudes. So, whereas in tropical areas we detected the lowest rates of herbivory and predation in highly populated areas compared to low-density populated areas, as one moves towards warm temperate latitudes, the difference in herbivory and predation between high and low human population density areas becomes negligible. Also, the pattern reverses in cold temperate and polar latitudes, where herbivory and predation increase in response to increasing human population density. Thus, the same increase of human population density has opposite effects on trophic interactions when comparing high and low latitudes in both hemispheres. This indicates a multi-trophic differential response to human population in response to a geographical pattern.

Latitude is affecting the strength of trophic interactions, but the direction of this effect is not uniform. While some point out to an increase in the strength of herbivory with latitude (Adams & Zhang, 2009), others have reported a maximum at intermediate latitudes (Kozlov *et al.*, 2015) or even a decrease with latitude (Pennings & Sillman, 2005; Meineke *et al.*, 2019). Our results confirm those by Pennings & Sillman (2005) and Meineke *et al.* (2019), at least for low populated areas, while these differences are not so apparent for high populated areas (Figure 3).

The opposite effects of urbanization on herbivory and predation in tropical versus cold latitudes can be explained in the view of the urban heat island effect (Kim, 1992). Cities can be up to 10 °C warmer than surrounding rural areas, which might positively affect ectotherm insects, particularly at cooler latitudes where temperature directly affects their performance. Thus, in cities at cooler latitudes, the time of activity of insects can be higher than in low density populated areas (Youngstead *et al.*, 2015), and this could counteract the adverse urbanization effects found in colder latitudes (Youngstead *et al.*, 2017). The heat island effect has also been demonstrated to disrupt Bergman's rule (which predicts smaller sizes in colder climates) in ectotherms, with cities at cold latitudes having bigger individuals than rural areas (Beasley *et al.*, 2018). In the other side, the increase of temperature may affect the survival of tropical insects as they tend to be thermal specialists adapted to environmental temperatures, relatively stable throughout the year (Sunday *et al.*, 2011). Tropical cities, where vegetation is active all year round, show less seasonal growth changes in response to the urban heat island effect than cities at higher latitudes, where artificial warmer conditions during winter can benefit the plants (Peng *et al.*, 2011) and the earlier springs could disrupt the plant-insect synchrony (Ren *et al.*, 2020). Also, cities can change the trophic dynamics by increasing resources and provide stability in limited resources ecosystems like deserts (Faeth *et al.*, 2005).

Birds' behaviour in response to human presence has been shown to change with latitude (Díaz *et al.*, 2021), with bird tolerance to human presence increasing with latitude (Poddubnaya *et al.*, 2019). This could help to understand the different responses of predation pressure by birds as human population density changes. At higher latitudes, birds tolerate better human presence, which added to the stable resources' availability in cities compared to natural areas (Anderies *et al.*, 2007), provokes the presence of higher abundances of birds, and this can lead to higher levels of bird predation. Alternatively, it is reasonable to expect the same geographical and disturbance patterns between insect herbivory and bird predation, since the abundance and diversity of predators (e.g., insectivorous birds) and preys (e.g., herbivorous insects) are controlled either via top-down (driven by consumers) or bottom-up (driven by resources) mechanisms (Polis *et al.*, 1997). Therefore, although for some bird predation the direct effects of human population density or latitude cannot be clear, its presence will be determined by that of the other groups of organisms on which they depend on (bottom-up mechanisms).

The interaction between urbanization and latitude on herbivory has been recently studied (Kozlov *et al.*, 2017; Meineke *et al.*, 2019; Moreira *et al.*, 2019) using latitudinal gradients in the northern hemisphere spanning 10° to 20°. Both in Europe (Kozlov *et al.*, 2017; Moreira *et al.*, 2019) and USA (Meineke *et al.*, 2019), there was a decrease in herbivory with increasing urban population but, contrary to our results, this effect was consistent throughout the latitudinal gradient. The discrepancies between the results reported in these studies and our findings might be related to the shorter latitudinal range covered by previous studies, the narrow population range covered (e.g. Meineke *et al.,* 2019), or the inclusion of human use categories instead of population density as a subrogate of human impact on the territory (e.g. Kozlov *et al.*, 2017; Moreira *et al.*, 2019). Indeed, previous studies investigating the effects of human pressure on herbivory and/or predation (Gering & Blair, 1999; Posa *et al.*, 2007; Cuevas-Reyes *et al.*, 2013; Ferrante *et al.*, 2014; Kozlov *et al.*, 2017; Eötvös *et al.*, 2018; Moreira *et al.*, 2019; Rivkin & Moura, 2020; Schwab *et al.*, 2020) are mostly based on categories of human use (i.e. urban, rural, pristine, managed, etc.), which are definitely not comparable among regions as the history of human use, degree of naturalization of a territory and management practices change remarkably across the globe. Comparison across studies based on human land use categories could therefore mask the effects of human impact on trophic interactions along latitudinal gradients.

Finally, it is proposed that cities could act as live simulators of climate change, currently representing the temperatures to be experienced in the future at the same latitude (Youngstead *et al.*, 2015; Frank & Just, 2020). Following this statement and based on our results, we could expect a decrease of bird predation rate and herbivory in response to climate change at tropical latitudes, no effects at temperate latitudes, and an increase of bird predation rate and herbivory in cold latitudes in the future. This could imply important effects on ecosystem services (e.g. nutrient cycling, pest control) that would affect tropical and boreal regions differently, producing an ecological imbalance that, added to the current biodiversity crisis, could lead to the worsening of socio-economic differences between regions.

Conclusions

Different global patterns in response to human population density were found depending on latitude. Higher human population density at high latitudes increases herbivory and predation pressure, but the opposite trend is observed at low latitudinal ecosystems. Such differences can be explained by the urban heat island effect. These differences between cold and tropical latitudes are important since it is predicted that the majority of the new big cities (5-10 million people) in the next ten years will be at tropical latitudes (United Nations, 2018), which will have detrimental consequences for trophic interactions and the ecosystem services they provide. These results open a new venue for studying human impacts on different ecosystem properties across latitudinal gradients.

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Supplementary material1

Table S1: Information about the prey-predator interaction papers used in this article.

Source	Range	Date	Days	Tree species	Attached	Lenght	Diameter
Mäntylä *et al.* (2008)	Finland	June 2007	14	*Betula pubescens*	Metal wire (Ø 0.35 mm)	2-3 cm	3-4 mm
Mäntylä *et al.* (2014)	Finland	June 2010	14	*Betula pubescens*	Metal wire (Ø 0.35 mm)	2-3 cm	3-4 mm
Maas *et al.* (2015)	Indonesia	June to July 2011	4	*Theobroma cacao*	Power glue	2 cm	4 mm
Roslin *et al.* (2015)	Global	June 2013 to August 2015	4	Several species	Power glue	3 cm	2.5 mm
Zvereva *et al.* (2019)	Global	May 2017 to December 2018	Up to 64	Several species	Wire (Ø 0.3–0.5 mm)	1.5-3 cm	4-5 mm
Murray *et al.* (2021)	Malasya	July to August 2016	3	Several species	Thin wire	NP	NP
Schwab *et al.* (2020)	Madagascar	October 2018	2	Vanilla	Pins	3.5 cm	5 mm
Zvereva *et al.* (2020)	North Europe	June 2016 to August 2019	Up to 17	*Betula*	Wire (Ø 0.3 mm)	2.8-3.2 cm	3.5-4 mm
Gomes *et al.* (2021)	USA	May -July 2018	5	Several species	Power glue	NP	NP
Hernández-Agüero *et al.* (2021)	Global	May 2017 to August 2020	Up to 50	Several species	Wire (Ø 0.3–0.5 mm)	1.3-3 cm	4-5 mm
Leuenberger *et al.* (2021)	USA	June 2015	6	*Viburnum lantanoides* and *Fagus grandifolia*	Power glue	2.2 cm	3.5 mm
Valdés-Correcher *et al.* (2021)	Europe	April 2018 to July 2019	14	*Quercus robur*	Metal wire (Ø 0.5mm)	3 cm	4 mm

Table S2: Information about the plant-herbivore interaction papers used in this article.

Source	Range	Date	Tree species
Kovlov *et al.* (2015)	Global	1961 to 2014	356 species
Mendes *et al.* (2021)	Global	March 2017 to February 2020	198 species
Hernández-Agüero *et al.* (2021)	Global	May 2017 to August 2020	34 species

Table S3: Coefficients of the best models and their standard deviation for both prey-predator and plant-herbivore trophic relations.

		Prey-Predator		**Plant-Herbivore**	
	Predictor	**Estimate**	**Std. Dev.**	**Estimate**	**Std. Dev.**
Random	Site	0.1125	0.3354	0.35841	0.5987
	Species/Genus			0.08096	0.2845
	Genus			0.08123	0.2850
Fixed	(Intercept)	-2.382320	0.27540	-2.34347	0.19304
	Log (Human Population)	-0.247253	0.076144	-0.09523	0.04486
	Abs (Latitude)	-0.003778	0.005654	-0.02548	0.00476
	Log (Human Population) * Abs (Latitude)	0.004106	0.001499	0.00318	0.00107

9. Discusión general

Se han investigado los mecanismos y patrones que explican la herbivoría por insectos y depredación por aves a distintas escalas espaciales. Se han estudiado los patrones de herbivoría de insectos en la región mediterránea sobre una de las especies de árboles más características de la cuenca Mediterránea, la encina (*Quercus ilex*), y a una escala inferior, a nivel de la meseta central de la Península Ibérica, se han establecido los mecanismos que aplican en la depredación por parte de aves en función de la coloración de la presa, así como los patrones temporales resultado de esta regulación. A nivel global, también se han explorado los mecanismos que afectan a las tasas diferenciales de depredación dependiendo del color de la presa, y a los patrones latitudinales que podrían estar explicando estas diferencias. Por último, y también a nivel global, se han estudiado los mecanismos que afectan tanto a herbivoría como a depredación, detectando patrones latitudinales y en respuesta de la presión humana en los ecosistemas.

Se han identificado 605 especies diferentes de artrópodos que utilizan la encina como recurso trófico y se ha podido establecer el tipo de relación trófica de la mayoría de ellas. Sin embargo, aunque se ha podido obtener la distribución del 80% de las especies, solo del 48% se tiene suficiente información respecto a su distribución para modelar su nicho climático. Además, solo se dispone del estado de conservación del 11% de ellas. La falta de conocimiento respecto a la distribución de especies invertebradas (Lomolino, 2004) o su ecología (Cardoso *et al.*, 2011) es algo ya reconocido. Además, se tiene constancia de que el conocimiento taxonómico de estas especies es muy reducido (Whittaker *et al.*, 2005), y muchas de las especies de artrópodos están aun por ser descubiertas. La encina es una especie de crecimiento lento, cuyo hábitat (la cuenca mediterránea) podría considerarse un área de recursos limitados, sobre todo limitada por la sequía estacional. Es por eso por lo que el nivel de desarrollo de defensa es elevado, como predice la hipótesis de disponibilidad de recursos (Coley *et al.*, 1985). Estas defensas de la planta obligarían a los herbívoros a adaptarse y llevar a cabo una coevolución rápida que conduce a su especialización trófica (Feeny, 1976). Esto explicaría por qué encontramos una diversidad tan alta (más de 600 especies) comparada con la diversidad de herbívoros asociada a otras especies del género *Quercus* (unas 300 especies; Southwood, 1961) distribuidas en zonas de mayor disponibilidad de recursos. Sin embargo, este numero de especies es bajo si lo comparamos con las de comunidades de invertebrados herbívoros de especies tropicales, que pueden llegar a ser hasta cuatro veces superior (Ødegaard, 2004).

Pese las limitaciones taxonómicas y de conocimiento, se han podido establecer agrupaciones por recursos tróficos consumidos que se corresponden en gran medida con los grupos taxonómicos, lo cual se ha podido corroborar con los análisis de señal filogenética, y que apoyan la hipótesis de "señal taxonómica" (Potapov *et al.*, 2019) lo que también estaría indicando un proceso de coevolución de las especies invertebradas herbívoras con la encina. Para algunos recursos tróficos, como las bellotas, esta señal taxonómica no es tan clara, con especies no relacionadas filogenéticamente, lo que puede explicarse por la hipótesis de la "similitud limitante" (Potapov *et al.*, 2019), agravada por la temporalidad del recurso trófico. Esto es que, al ser un recurso tan limitado en el tiempo, y con una competencia tan grande, no permite la especiación como si lo hacen otras partes de la planta. Se ha podido establecer una similitud de nicho climático con la encina del 20% de las especies evaluadas, lo que supone un mayor grado de adaptación que el resto, y que también estaría explicado por la coevolución mediada por la planta, a través de mecanismos de abajo (la planta) a arriba (el herbívoro) (Leppänen *et al.*, 2013). Esta similitud de nicho refleja especificidad de especie hospedadora (Arnal *et al.*, 2019). Sin embargo, no es el único factor que regula la distribución de estas especies, que se suele ver aun más restringida por sus propios requerimientos climáticos (Du *et al.*, 2020).

El modo en la que las especies de herbívoros se distribuyen a nivel regional o a nivel hospedador puede estar también regulado por los depredadores mediante mecanismos de arriba abajo, "top-down" (Leppänen *et al.*, 2013). La depredación es mayor en zonas más abiertas de la planta (Dial y Roughgarden, 1995) y puede verse afectada por señales visuales, dependiendo de, por ejemplo, el color de fondo de la parte de la planta utilizada por el herbívoro, el cual es fundamental para la eficacia del camuflaje (Cott, 1940), pero también afecta a la eficacia de las señales aposemáticas (Ruxton *et al.*, 2004).

Respecto a estas señales, se ha podido demostrar la eficacia antidepredatoria del color amarillo, ya propuesto anteriormente como una señal aposemática (Iniesta *et al.*, 2016; Lawrence y Nooan, 2018) y del también efecto reductor de la depredación del color verde en las presas, en este caso al tratarse de un color críptico ante un fondo también verde dominado por hojas (Cott, 1940). Además, la especie de árbol también supuso diferencias en cuanto a la intensidad de esta relación trófica, lo cual se podría explicar por diferencias de conspicuidad de las señales ya sean de camuflaje (Edmunds y Grayson, 1991) o de aposematismo (Ruxton *et al.*, 2004), aunque podría también estar explicado por mecanismos de abajo a arriba, "bottom-up", por una mayor concentración de sustancias químicas antidepredatorias (Coley, 1988), como es el caso de las jaras (*Cistus ladanifer*) y la presencia de flavonoides (Sosa *et al.*, 2004). No es esperable una depredación elevada de artrópodos herbívoros de una planta con una defensa química tan marcada como la jara, ya que se esperaría que se hubiera producido una coevolución tanto de los herbívoros como de sus depredadores para evitar las consecuencias perjudiciales de esta defensa química (Feeny, 1976).

La eficacia de las señales antidepredatorias no se ve modificada en el tiempo, pero si se observa un patrón bimodal de la intensidad de la depredación en todos los colores. Entre otras explicaciones, como el aprendizaje de las aves al no obtener recompensa de la depredación de las larvas o la llegada de aves migratorias o juveniles (Mappes *et al.*, 2014), cabría esperar una coevolución de la depredación de las aves en respuesta a la estacionalidad de la presencia de sus presas (Coley, 1996), que puede estar mediada por el desarrollo de nuevas hojas (Aide, 1993).

Las señales visuales estudiadas tampoco se han visto afectadas por componentes geográficos a escala regional, posiblemente por el pequeño rango latitudinal utilizado. Sí se detectaron estas diferencias, excepto para el color amarillo, a nivel global. El color amarillo supone una señal aposemática que evita la depredación por aves y artrópodos independientemente de la latitud. No sucede lo mismo con otro tipo de señales visuales, como las coloraciones claras u oscuras no aposemáticas, que presentan variación latitudinal en su vulnerabilidad, principalmente, por el entorno en el que se sitúan (Cott, 1940) por diferencias en su detectabilidad en función de la luminosidad (Cheng *et al.*, 2018). Pese a que se acepta que la intensidad de las interacciones tróficas es mayor en áreas tropicales que en latitudes superiores (Coley y Barone, 1996; Schemske *et al.*, 2009), este patrón solo se detectó para depredadores artrópodos, al igual que en estudios anteriores (Roslin *et al.*, 2017). Sin embargo, la intensidad de la depredación por aves aumentó con la latitud, patrón que también se repite al analizar los datos publicados en 12 estudios, aunque solo en lugares de estudio con alta densidad de población, mientras que para zonas con baja densidad de población el patrón fue el inverso. Esto es resultado de la interacción entre el efecto de la latitud sobre la depredación y el de la perturbación humana.

No existe un consenso acerca de cómo el impacto humano afecta a la depredación por aves (Posa *et al.*, 2007; Eötvös *et al.*, 2018), al igual que la herbivoría por insectos (Dreistadt *et al.*, 1990; Hanks y Deno, 1993; Cregg y Dix, 2001; Kozlov *et al.*, 2017; Meineke *et al.*, 2019; Moreira *et al.*, 2019). Sin embargo, los estudios realizados en los últimos años apuntan tanto a una reducción de la herbivoría como de la depredación en respuesta a la presión humana (Eötvös *et al.*, 2018; Kozlov *et al.*, 2017; Meineke *et al.*, 2019; Moreira *et al.*, 2019), lo cual podría estar reflejando un aumento el impacto humano en ciudades por su rápido crecimiento. En los últimos 20 años la población humana en ciudades respecto al total de la población ha pasado del 45% al 55% (Banco Mundial, 2021). Con ese aumento, los impactos principales asociados a las ciudades, como la contaminación del aire, cambio de uso de suelo o el clima (Bai *et al.*, 2017), pueden haberse visto también aumentados. En ciudades, el sobrecalentamiento por la presencia de asfalto y edificios puede suponer un aumento de 10 ºC (Kim, 1992), lo que tiene consecuencias directas sobre las redes tróficas (Miles *et al.*, 2019), y podría estar explicando que se produzcan patrones opuestos tanto de herbivoría como de depredación entre zonas poco pobladas y zonas densamente pobladas. En zonas de latitudes altas, este cambio del clima de las ciudades podría beneficiar a los insectos herbívoros que presentarían limitaciones climáticas dentro de las ciudades inferiores a las de zonas poco pobladas, aumentando tanto la intensidad de las interacciones de herbivoría, mediada por procesos “top-down”, como de depredación por aves, mediada por procesos “bottom-up”.

9.1.Referencias

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10. Conclusiones

1. La encina alberga una gran cantidad de especies de artrópodos herbívoros, lo que respalda su papel como especie clave en los bosques mediterráneos.
2. Las especies estrechamente relacionadas filogenéticamente entre sí tienen estrategias de alimentación similares, lo que apoya la hipótesis de la "señal taxonómica".
3. Existe un grado moderado de especificidad del hospedador entre las especies herbívoras de la encina (aproximadamente el 20%), pero no hay diferencias de especificidad del hospedador por grupos tróficos.
4. Las bajas tasas de ataque en larvas amarillas son consecuencia del aposematismo, mientras que las bajas tasas de ataque larvas verdes se deben a la cripsis.
5. La rápida disminución de las tasas de ataque a lo largo del tiempo es probablemente el resultado del aprendizaje, y el aumento de los ataques en los meses más cálidos podría explicarse por el aumento de polluelos y la aparición de adultos migrantes.
6. La depredación de insectos herbívoros por aves aumenta desde el ecuador hacia los polos, en una dirección opuesta a la depredación de artrópodos y opuesta a las predicciones de la hipótesis de interacción biótica latitudinal. Además, se ven afectados de manera diferente por el color de la presa en diferentes ambientes.
7. Una mayor densidad de población humana en latitudes elevadas aumenta la presión de la herbivoría y la depredación.
8. Una mayor densidad de población humana en latitudes bajas disminuye la presión de herbivoría y depredación.
9. El efecto de interacción entre la latitud y la densidad de población sobre las interacciones tróficas puede explicarse por los cambios climáticos producidos por el efecto isla de calor de las ciudades.